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## The Ophionine Wasps of Hawaii (Hymenoptera: Ichneumonidae)

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**Abstract.**—Hawaii's largest group of Ichneumonidae, the Ophioninae, is reviewed. Thirty species are recognized in one genus, *Enicospilus* Stephens. A key to species and a table of distributions indicating 26 new island records are provided. The following seven species are described as new: *Enicospilus ashei*, *Enicospilus dorsolineatus*, *Enicospilus elekino*, *Enicospilus hainesi*, *Enicospilus gladiator*, *Enicospilus minimus*, and *Enicospilus petilus*. *Enicospilus tyrannus* Perkins 1910 is newly synonymized with *Enicospilus longicornis* Ashmead 1901. The following genera are synonymized with *Enicospilus*: *Abanchogastra* Perkins 1902, *Banchogastra* Ashmead 1900, and *Pycnophion* Ashmead 1900. Replacement names are *Enicospilus blackburni* (= *Enicospilus molokaiensis* Ashmead 1901) and *Enicospilus swezeyi* (= *Pycnophion fuscipennis* Perkins 1910).

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"The variability of many of the Hawaiian Ophionini is so excessive, that if similar variation occurs in other tropical countries, the group may well prove one of the most difficult of entomological studies."

— R. C. L. Perkins 1915

Perkins' prescience indeed foretold a challenge to systematic entomologists. Yet, at the time he couldn't have fully known the magnitude of the problem. The ophionine genus *Enicospilus* alone is now represented by an excess of 650 described species (Yu and Horstmann 1997), with an untold diversity concentrated in tropical areas and particularly large radiations occurring in Madagascar and New Guinea (Gauld and Mitchell 1981). Likewise, in the most remote of tropical areas, the Hawaiian Islands, *Enicospilus* has flourished and given rise to an array of species that comprise the majority of Hawaii's native ichneumonids. Many of these are notable for morphologies and habits that differ strikingly from an otherwise homogeneous *Enicospilus* outside the islands (Gauld 1985, Bennett 2004). Such features include a variety of ovipositor lengths and shapes,

drastic reductions in body size, stout body forms, and, concomitant with diurnal behavior, smaller eyes and dark coloration (e.g. Figs 1, 4E). Woefully little is known about the biology of most Hawaiian *Enicospilus* species, yet from the variety of ovipositor types exhibited, and from one host record, it is evident that the evolution of this morphological exuberance is at least in part related to the attack of novel hosts. As koinobiont endoparasitoids, ophionine species are generally known to parasitize large, exposed caterpillars, particularly of the families Noctuidae, Lasiocampidae, Lymantriidae, Saturniidae, Geometridae, Arctiidae, and Sphingidae (Gauld 1988). The habits of several Hawaiian species are indeed consistent with this. Swezey (1931, 1954), however, reared *Enicospilus swezeyi* (Fig. 1), a species with a long, straight ovipositor from the cosmopterigid *Hypomocoma chilonella* Walsingham concealed within *Rubus* stems. There are as of yet no host data for additional species with long, straight ovipositors or for those with long, curved ovipositors.

As is the case for many Hawaiian insects, the first ophionine wasps were collected in



Fig. 1. *Enicospilus swezeyi*.

Hawaii by the minister naturalist Thomas Blackburn. During the years 1877–1883, he sent many insects to specialists in London including four ophionine wasps to Cameron who described them as male-female pairs of two species in the genus *Ophion* (Cameron 1883), though the original series actually contained four distinct species (Perkins 1915). These were appropriately transferred to *Enicospilus* (or the unjustified form *Henicospilus*) in subsequent catalogs (Szépligeti 1905, Morley 1912). Meanwhile, Ashmead was describing new species and genera of Hawaiian Ophioninae (Ashmead 1900, 1901) sent to him by Perkins who later complained bitterly about Ashmead's

"extraordinary" treatment of conspecific individuals, his mixtures of species under single names, and his habit of designating as types, individuals from locations other than those for which such species were named (the latter can be explained given that Ashmead didn't designate holotypes per se, but rather often wrote "type" on each individual of his syntype set, which in some cases represented multiple islands). Perkins' revision (1915) recognized six genera of Hawaiian Ophioninae and fully treated the species of *Enicospilus*, providing a key and noting many important characters. Cushman (1944) attempted to use subgenera for a number of taxa (including



two of Perkins' genera) as a means of recognizing the increasing number of aberrant derivatives of *Enicospilus* in Hawaii. His use of subgenus was not followed, but his key works well, and his review was important in showing that a good number of names were confused for widespread, polymorphic species. Since Cushman's work, species-level taxa have generally remained stable, but the generic classification of these species has fluctuated between the opinions of several authors. Townes (1945) further reduced the number of genera by synonymizing *Abanchogastra* and *Banchogastra* under *Enicospilus*. Cushman (1947) recognized *Pycnophion* and *Banchogastra* as genera, but not *Abanchogastra*. Townes et al. (1961) took the same position as Townes (1945), but later Townes (1971) also raised *Banchogastra* to genus. That such confusion would reign regarding the genus-group status of these taxa is a result of the evolution of highly apomorphic morphologies and the subjectivity inherent in deciding which derivatives are sufficiently different to warrant removal from *Enicospilus*. The phylogenetic analysis of Gauld (1985) provided the first congruence test to indicate that *Pycnophion*, *Banchogastra*, and *Abanchogastra* were indeed apomorphic, insular lineages derived from within *Enicospilus*. Recent and forthcoming cladistic analyses have upheld this view (Bennett 2004, in prep.). Gauld (1985), however, maintained the genus-rank status of these groups owing to his view that it was impractical to include highly aberrant derivatives within an otherwise morphologically and behaviorally homogeneous *Enicospilus*; this arrangement was upheld in a recent catalogue of Ichneumonidae (Yu and Horstmann 1997). Herein is proposed a classification that, for the first time, reflects the *Enicospilus* ancestry of all Hawaiian Ophioninae. Descriptions of new taxa, a summary of species and their distributions (Table 1), and an updated key to species are also provided.

## METHODS

Morphological terminology, indices, and species description format generally follow Gauld and Mitchell (1981) and Gauld (1988); select additional terms are described by Townes (1969). Integumental sculpture terminology follows Harris (1979). Mandibles are described in reference to a horizontal position as opposed to projecting ventrally. Malar space is measured as the shortest distance between a point just above the anterior dorsal margin of the mandible and the eye. Fore wing length does not include the tegula. The cubital index (CI) of the hind wing is newly defined as the distance between the junction of Cu1 (second abscissa) and cu-a and the junction of cu-a and 1A along an imaginary line between the junction of M+Cu and Cu1 (first abscissa) and the junction of cu-a and 1A (Fig. 5D-b) divided by the latter imaginary line (Fig. 5D-a). The ventral face of the mesopleuron is described as the "mesosternum." The "lower metapleuron" is used to mean that part of the metapleuron ventral and posterior to the propodeal spiracle. The angle of the anterior mesoscutum and the posterior declivity of the scutellum are estimated with reference to a horizontal line taken as a line between the cervix and the posterior foramen of the propodeum. Hind coxa length is measured from the basal constriction to the dorsal apical-most point in lateral view. Tergal numbers are in reference to the metasoma and not the true abdomen. The length of T2 is measured in lateral view between anterior and posterior dorsal midpoints.

Many of the characters previously pointed out as critical to the delineation of ophionine species (Gauld and Mitchell 1981, Gauld 1988) are likewise important in Hawaiian *Enicospilus*. Paramount among these is the form of the hairless region of the discosubmarginal cell, or fenestra, and the sclerites often accompanying it. On this basis alone, many species can be identified. Also important are the mandible shape,

Table 1. Distributions of Hawaiian Ophioninae. New island records indicated by \*. Lower case “x” denotes unverified literature records.

| Species  | Kauai | Oahu | Molokai | Lanai | Maui | Hawaii |
|--|-------|------|---------|-------|------|--------|
| <i>Enicospilus ashei</i> Bennett               | X*    |      |         |       |      |        |
| <i>Enicospilus bellator</i> Perkins 1915       |       | x    | x       |       | X    | X      |
| <i>Enicospilus blackburni</i> Bennett          | X     | X    | X       | x     | X    | X      |
| <i>Enicospilus castaneus</i> Ashmead 1901      |       | X    | X       | X     | X*   | X      |
| <i>Enicospilus debilis</i> (Perkins 1902)      |       | X    |         |       | X    | X      |
| <i>Enicospilus dispilus</i> Perkins 1902       | X     | X    | X       | X*    | X    | X      |
| <i>Enicospilus dorsolineatus</i> Bennett       |       |      |         |       |      | X*     |
| <i>Enicospilus elekino</i> Bennett             |       |      |         |       | X*   |        |
| <i>Enicospilus ferrugineus</i> (Perkins 1915)  |       | X*   |         |       | X    |        |
| <i>Enicospilus fullawayi</i> Cushman 1944      | X     | X*   |         |       | X*   | X*     |
| <i>Enicospilus gladiator</i> Bennett           | X*    |      |         |       |      |        |
| <i>Enicospilus hainesi</i> Bennett             |       | X*   |         |       |      |        |
| <i>Enicospilus hawaiiensis</i> (Ashmead 1900)  |       |      |         |       |      | X      |
| <i>Enicospilus kaalae</i> Ashmead 1901         | X     | X    | X       |       | X    | X      |
| <i>Enicospilus kauaiensis</i> (Ashmead 1901)   | X     |      | X*      |       |      |        |
| <i>Enicospilus lineatus</i> (Cameron 1883)     | X     | X    | X       | x     | X    | X      |
| <i>Enicospilus longicornis</i> Ashmead 1901    | X     | X    | X*      |       | X    | X      |
| <i>Enicospilus melanochromus</i> Perkins 1915  | X*    | X    | X*      |       | x    | X*     |
| <i>Enicospilus minimus</i> Bennett             |       | X*   |         |       |      | X*     |
| <i>Enicospilus molokaiensis</i> (Ashmead 1900) | X     |      | X       |       | X    |        |
| <i>Enicospilus niger</i> (Ashmead 1900)        |       |      |         |       |      | X      |
| <i>Enicospilus nigrolineatus</i> Ashmead 1901  | X     | X    | X       | X     | X    | X      |
| <i>Enicospilus orbitalis</i> (Ashmead 1901)    | X     | X    | X       |       | X    | X      |
| <i>Enicospilus perkinsi</i> Cushman 1944       | X     |      |         |       |      |        |
| <i>Enicospilus petilus</i> Bennett             |       |      | X*      |       | X*   | X*     |
| <i>Enicospilus pseudonymus</i> Perkins 1915    | X*    |      |         |       | X    |        |
| <i>Enicospilus swezeyi</i> Bennett             | X     | X*   |         |       | X    |        |
| <i>Enicospilus variegatus</i> Ashmead 1901     |       |      |         |       |      | X      |
| <i>Enicospilus vitreipennis</i> (Perkins 1910) | X*    | X*   |         |       | X    | X*     |
| <i>Enicospilus waimeae</i> Ashmead 1901        | X     |      |         |       |      | x      |
| Total 30                                       | 18    | 17   | 13      | 5     | 19   | 20     |

upper tooth shape, malar space, size and shape of the compound eye and ocelli, shape and sculpture of the scutellum, hind wing venation, pretarsal claws, propodeal sculpture, metasoma shape, ovipositor shape, and color. The posterior propodeal carina is not known to occur in any Hawaiian *Enicospilus*; its absence is not repeated in the descriptions.

Institutions and their acronyms are as follows: American Entomological Institute, Gainesville, FL, USA (AEIC); Bernice Pauahi Bishop Museum, Honolulu, HI, USA (BPBM); Canadian National Collection, Ottawa, Ontario, Canada (CNCI); The Natural History Museum, London, UK (BMNH); The United States National Museum (USNM); University of Hawaii, Manoa, HI, USA (UHM).

KEY TO SPECIES OF HAWAIIAN OPHIONINAE

1. Hind wing with first abscissa of Rs < 2.0× as long as rs-m (Fig. 7E), 1A absent and second abscissa of Cu1 present only as a short stub; very small, fore wing length about 5 mm or less . . . . . *E. minimus*

- Hind wing with first abscissa of Rs  $> 2.0\times$  as long as rs-m, both 1A and second abscissa of Cu1 distinct (Fig. 5D); larger, fore wing at least 6 mm, usually much larger ..... 2
- 2. Fore wing discosubmarginal cell with or without sclerites, with distinct fenestra present; posterior transverse carina of mesosternum present medially ..... 3
- Fore wing discosubmarginal cell without sclerites, fenestra absent (Figs 23, 29), or if present, then only as a poorly defined region of reduced pubescence without distinct lower margin (Figs 17, 22, 27); posterior transverse carina of mesosternum absent medially, or if present then weak ..... 22
- 3. Fore wing with 1m-cu usually evenly curved or arched, if angulate and swollen medially, then only slightly so (Figs 10, 21, 26); ovipositor short and straight or curved, about  $1.2\times$  length of T2 or less ..... 4
- Fore wing with 1m-cu medially strongly angulate, swollen (Fig. 6), or with short stub (Figs 5C, 15); ovipositor long and straight, about  $1.8\times$  length of T2 or more ..... 29
- 4. Metasoma extremely slender, dorsomedial length of exposed portion of T5 in female, T4 in male, greater than lateral depth ..... 5
- Metasoma not as slender, dorsomedial length of exposed portion of T5 in female, T4 in male, less than lateral depth ..... 8
- 5. Fore wing discosubmarginal cell with 2 sclerites, proximal one very large (Fig. 8D) ..... *E. petilus*
- Fore wing discosubmarginal cell without sclerites, or if one present, then not approaching in size that of above ..... 6
- 6. Fore wing discosubmarginal cell with fenestra broad, posterior margin extending beyond midpoint between Rs+2r and 1m-cu, with a single, linear sclerite at proximal, ventral margin of fenestra (Fig. 14) ..... *E. fullawayi*
- Fore wing discosubmarginal cell with fenestra round and smaller, ventral margin not extending beyond midpoint between Rs+2r and 1m-cu, if sclerite present, then spherical ..... 7
- 7. Fore wing discosubmarginal cell without a sclerite (Fig. 25) ..... *E. orbitalis*
- Fore wing discosubmarginal cell with a single sclerite (Fig. 26) ..... *E. perkinsi*
- 8. Mesosoma yellow or yellow and black ..... 9
- Mesosoma brown, red, orange, or black ..... 12
- 9. Mandible with a heavily setose, diagonal groove (Fig. 36); fore wing discosubmarginal cell with 2 or 3 sclerites, central sclerite oval or triangular and medially placed in fenestra (Fig. 20); ovipositor downcurved ..... *E. longicornis*
- Mandible with at most a weakly to moderately setose, diagonal line (Fig. 37); fore wing discosubmarginal cell with 1 or 2 sclerites, if 2, then the second positioned along ventral margin of fenestra; ovipositor straight ..... 10
- 10. Fore wing discosubmarginal cell with 2 sclerites (the second may be translucent; showing weakly in figure) (Fig. 24); hind femur yellow or yellowish-brown throughout; propodeum in large part black; metasoma yellow or yellowish-brown except for lateral dark line ..... *E. nigrolineatus*
- Fore wing discosubmarginal cell with 1 or 2 sclerites (Figs 3C, 28); hind femur as described above or with apex black; propodeum as above or yellow to yellowish brown throughout; metasoma yellow, yellowish-brown, or black, never with lateral dark line ..... 11
- 11. Malar space  $0.4\text{--}0.5\times$  basal mandibular width; metasoma mostly yellow or yellowish-brown, except for a dorsomedial dark line ..... *E. dorsolineatus*
- Malar space  $0.3\text{--}0.4\times$  basal mandibular width; metasoma mostly black, not forming a dorsomedial line ..... *E. variegatus*
- 12. Fore wing discosubmarginal cell with fenestra large, extending posteriorly  $3/4$  or more the distance between Rs+2r and 1m-cu, and apically to about midpoint of Rs+2r or further; with 1 small, oval or attenuated sclerite, positioned at proximal posterior

|     |  |                         |
|-----|--|-------------------------|
|     | margin of fenestra, nearer 1m-cu than Rs+2r (Figs 10, 16, 21); female S7 enlarged (Fig. 32); ovipositor straight   | 13                      |
| -   | Fore wing discosubmarginal cell with fenestra smaller, posterior margin extending about 2/3–1/2 or less the distance between Rs+2r and 1m-cu, apically to about midpoint of Rs+2r or less; if alar sclerite(s) present, then variously shaped and positioned; female S7 not enlarged (Fig. 31), or if enlarged, then ovipositor downcurved (Fig. 33) | 15                      |
| 13. | Fore wing with 1m-cu not thickened or angled medially (Fig. 16), alar sclerite spherical, not attenuated apically; middle segments of metasoma deep reddish or orangish-brown, usually strongly contrasted with much darker petiole and apical segments  | <i>E. kaalae</i>        |
| -   | Fore wing with 1m-cu usually at least slightly thickened and/or angled medially (Figs 10, 21), alar sclerite often attenuated apically; middle segments variable in color but usually not strongly contrasted with petiole and apical segments   | 14                      |
| 14. | Fore wing with 1m-cu usually slightly angled medially; fenestra not or poorly defined proximal of sclerite (Fig. 10); aedeagus slender apically; light reddish-brown to orange in color  | <i>E. blackburni</i>    |
| -   | Fore wing with 1m-cu not angled medially; fenestra broad and well defined proximal of sclerite; aedeagus bulbous apically; usually dark in color   | <i>E. melanochromus</i> |
| 15. | Dorsal surface of scutellum more or less flat, rugulose and/or coarsely pitted, scutellar carinae strong, often produced above medial part of scutellum; malar space 0.3–0.7× basal mandibular width; male apical tarsomere parallel-sided or swollen basally in dorsal view, strongly curved in lateral view  | 16                      |
| -   | Dorsal surface of scutellum convex and lightly punctate, scutellar carinae weak or moderate, not produced above medial part of scutellum; malar space 0.1–0.4× basal mandibular width; apical tarsomere of male evenly broadened apically in dorsal view, straight to moderately curved in lateral view  | 18                      |
| 16. | Fore wing with fenestra very small, without a distinct sclerite but with a faint sclerotization or pigmentation at posterior margin (Fig. 9); ratio of head height to width in frontal view about 1.1  | <i>E. bellator</i>      |
| -   | Fore wing with fenestra at least slightly larger, with 1 or 2 sclerites, or rarely with none or a vestigial proximal sclerite; ratio of head height to width in frontal view = 0.9–1.1   | 17                      |
| 17. | Malar space long, 0.4–0.7× basal mandibular width; flagellum of female short, length equal to or less than that of fore wing; fore wing fenestra usually with 1 sclerite (Fig. 11), occasionally with none or with a second vestigial, medially placed sclerite  | <i>E. castaneus</i>     |
| -   | Malar space 0.3–0.5× basal mandibular width; flagellum of female longer, length equal to or greater than that of fore wing; fore wing fenestra usually with 2 distinct sclerites (Fig. 13), occasionally the second, medially placed sclerite is weak, or a third sclerite at distal margin of fenestra is apparent                                  | <i>E. dispilus</i>      |
| 18. | Fore wing discosubmarginal cell without an alar sclerite   | 19                      |
| -   | Fore wing discosubmarginal cell with at least 1 alar sclerite  | 20                      |
| 19. | Orange except apical segments of metasoma black; mandible slender, with upper tooth medially swollen and long, 1.4–1.6× length of lower tooth (Fig. 2D)  | <i>E. ashei</i>         |
| -   | Usually brown or reddish-brown, apex of metasoma at most slightly darker; mandible moderately stout, upper tooth not conspicuously swollen medially, 1.1–1.6× length of lower tooth  | <i>E. lineatus</i>      |
| 20. | Mandible with a heavily setose, diagonal groove (Fig. 36); fore wing discosubmarginal cell with a large triangular proximal sclerite, a distinct central sclerite, and often a third pale sclerite outlining distal ventral margin of fenestra (Fig. 20); ovipositor downcurved (Fig. 33).   | <i>E. longicornis</i>   |

- Mandible with at most a moderately setose, diagonal line (Fig. 37); fore wing discosubmarginal cell usually with a single variously sized sclerite, rarely with a second medial sclerite, never with a third apical sclerite; ovipositor straight ..... 21
- 21. Fore wing discosubmarginal cell with a single, extremely large proximal sclerite (Fig. 30). ..... *E. waimeae*
- Fore wing discosubmarginal cell with proximal sclerite smaller, at most as in Fig. 19, usually much smaller (Fig. 18) ..... *E. lineatus*
- 22. Metasoma more or less black, rarely with a deep reddish tint; fore wing discosubmarginal cell without a sclerite ..... 23
- Metasoma of typical brown, red, or orange coloration; fore wing discosubmarginal cell with or without a sclerite ..... 28
- 23. Head entirely black; compound eye highly reduced (Figs 4A, B); propodeum evenly colliculate, without rugae; mid coxa with ridges dorsomedially ..... *E. elekino*
- Head entirely black or with pale areas; if compound eye reduced, then propodeum coarsely rugose, areolate, or rugostriate; mid coxa at most slightly wrinkled dorsomedially ..... 24
- 24. Ovipositor shorter than petiole; compound eye highly reduced (cf. Figs 4A, B); fore wing discosubmarginal cell usually densely setose throughout, usually with no trace of a fenestra (Figs 23, 29); propodeum coarsely rugose, areolate, or rugostriate, with strong anterior transverse carina ..... 25
- Ovipositor about twice petiole length or more; compound eye not reduced; fore wing discosubmarginal cell markedly less setose, especially proximally, often with a vestigial fenestra or poorly defined area of reduced pubescence below Rs+2r (Figs 17, 22); propodeum evenly colliculate or moderately rugose, if the later, then anterior transverse carina absent ..... 26
- 25. Petiole very compact, bulbous apically, ventral posterior midpoint positioned far anterior such that the ratio of ventral to dorsal length = about 0.4 or less (Fig. 34) (measured in lateral view from sub-basal narrowing); T2 wider than long in dorsal view; fore wing dark brown anteriorly, highly contrasted with lighter posterior apical area ..... *E. niger*
- Petiole not as compact, flatter apically, ventral posterior margin usually positioned further posterior such that the ratio of ventral to dorsal length = about 0.5 (Fig. 35); T2 usually longer than wide in dorsal view; fore wing variously light or dark, anterior and posterior apical area usually of similar hue or only slightly contrasted ..... *E. vitreipennis*
- 26. Ovipositor straight; anterior transverse carina of propodeum absent; setae of dorsomedial propodeum posteriorly directed; propodeum moderately rugose, at least posteriorly; mesosoma usually mostly red ..... *E. swezeyi*
- Ovipositor upcurved; anterior transverse carina of propodeum present or absent; setae of dorsomedial propodeum erect or curved anteriorly; propodeum evenly colliculate throughout; mesosoma usually mostly black ..... 27
- 27. Head and mesosoma all black ..... *E. kauaiensis*
- Head and/or mesosoma with pale or red areas ..... *E. molokaiensis*
- 28. Mandible with teeth stout, upper tooth shorter than lower tooth; posterior mesonotum and scutellum with lateral, longitudinal depressions; relatively large, fore wing length at least 11.5 mm ..... *E. pseudonymus*
- Mandible with teeth slender, upper tooth longer or about equal in length to lower tooth; posterior mesonotum and scutellum evenly flat or convex; small, fore wing length about 9.0 mm or less ..... *E. debilis*
- 29. Fore wing discosubmarginal cell without a sclerite (Figs 6, 15) ..... 30
- Fore wing discosubmarginal cell with a distinct, medially placed sclerite (Fig. 5C). ..... *E. gladiator*

- |     |  |                       |
|-----|--|-----------------------|
| 30. | Fore wing 1m-cu medially without a distinct stub (Fig. 6E) ..... | <i>E. hainesi</i>     |
| -   | Fore wing 1m-cu medially with a distinct stub (Fig. 15) .....    | 31                    |
| 31. | Dark brown in color; Hawaii Island .....                         | <i>E. hawaiiensis</i> |
| -   | Red or orange in color; Oahu, Maui .....                         | <i>E. ferrugineus</i> |
- 

## SYSTEMATICS

### *Enicospilus ashei*, new species

Fig. 2A–F

**Diagnosis.**—This species can be recognized by the combination of a slender mandible and a long, medially swollen upper tooth (Fig. 2D), distinct fenestra lacking sclerites (Fig. 2F), and general orange to brownish-orange coloration, becoming black on apical metasomal segments.

**Description.**—Length of fore wing 9.5–13.1 mm in female, 11.0–12.8 mm in male.

**Head:** Mandible slender, slightly twisted, medially and apically more or less parallel-sided; basal ventral margin moderately to strongly narrowed; outer surface with distinct basal concavity, setae scattered or fairly concentrated medially, very lightly punctate and generally smooth; upper tooth long, swollen medially, 1.4–1.6× as long as lower tooth, about equal in width to lower tooth at base (Fig. 2D). Labrum 0.2–0.3× as long as broad, apical margin broadly rounded to broadly pointed. Malar space 0.1–0.2× as long as basal mandibular width. Clypeus in profile weakly to moderately convex, proximal margin weakly to moderately distinct from lower face; in frontal view 1.6–2.0× as broad as long, sparsely and lightly punctate, apical margin medially flat or broadly rounded. Lower face 0.6–0.7× as broad as long, lightly to moderately punctate, evenly so or somewhat more coarse or dense medially. Compound eye large and strongly convex, head width in frontal view 1.1–1.3× length (Fig. 2A). Gena with setae short, inconspicuous and declined forward; in dorsal view somewhat narrow and constricted to moderately rounded behind compound eye (Fig. 2B); GOI = 2.4–3.4. Ocelli moderately large,

lateral ocellus removed from compound eye by 0.1× its diameter; FI = 0.5–0.7. Occipital carina dorsally flat or broadly rounded, ventrally joining or ending short of hypostomal carina. Flagellum in female 1.2–1.3× length of fore wing, with 48–51 segments, mid segment 1.9–2.3× as long as broad; in male 1.3–1.5× length of fore wing, with 55–57 segments, mid segment 1.7–2.1× as long as broad. **Mesosoma:** Mesoscutum in profile rounded anteriorly, angled by 70°–90°; notauli weak or not apparent. Scutellum in dorsal view 1.1–1.3× as long as anteriorly broad, upper surface moderately flat to moderately convex, lightly punctate; with lateral carinae moderately convergent, extending 3/5–4/5 scutellar length; with posterior declivity angled by 30°–45° in profile. Mesopleuron punctate to rugulostriate (some individuals less sculptured or evenly punctate medially); scrobe distinct, may or may not be set in shallow depression that, when present, may extend dorsally; speculum well defined as a dorsal posterior swelling; mesopleural sulcus with weak transverse ridges; epicnemial carina strong, complete medioventrally. Mesosternum without lateral longitudinal depression; with posterior transverse carina complete medioventrally. Lower metapleuron moderately convex, punctostriate to rugulostriate. Propodeum in profile weakly and evenly rounded throughout; pubescence with setae posteriorly declined, straight or with some posterior ones apically curved; spiracle narrowly oval; anterior furrow fairly shallow to moderately strong, rugulose to rugulostriate, anterior area 0.1–0.2× total propodeal length; anterior transverse carina absent, posterior transverse carina absent; spiracular area minutely colliculate; posterior area rugose. Separation between



propodeum and lower metapleuron indicated by weak furrow, slightly carinate anteriorly in some specimens examined. Fore wing (Fig. 2F) with pterostigma fairly abruptly to somewhat evenly narrowed distally; discosubmarginal cell without sclerites (vestiges apparent in some individuals), fenestra moderately long and moderately wide, extending apically to about  $1/3$  the length of  $Rs+2r$  and posteriorly to nearer  $1m-cu$  than  $Rs+2r$ ;  $Rs+2r$  thickened in basal half, slightly to moderately sinuous, evenly tapered and slightly concave medially;  $Rs+M$  slightly to strongly arched in basal half;  $1m-cu$  strongly arched, slightly thickened medially in some specimens examined;  $AI = 1.7-2.6$ ;  $CI = 0.3-0.5$ ;  $ICI = 0.3-0.5$ ;  $SDI = 1.0-1.3$ ;  $cu-a$  anterior of  $Rs+M$  by  $0-0.7$  length of  $cu-a$ ;  $1^{st}$  subdiscal cell sparsely pubescent distally and/or medially or nearly devoid of setae throughout. Hind wing with 5–7 distal hamuli in distal set;  $1^{st}$  abscissa of  $Rs$  slightly concave or more or less straight basally,  $2^{nd}$  abscissa more or less straight;  $2^{nd}$  abscissa of  $Cu1$  positioned midway or slightly ventral of midpoint between  $M$  and  $1A$ . Fore leg with tibia  $9.4-10.3\times$  as long as wide, without an array of subapical spines. Mid leg with coxa smooth or slightly wrinkled medially, inner tibial spur  $1.3-1.5\times$  as long as outer spur. Hind leg coxa in lateral view  $1.8-1.9\times$  as long as deep, finely imbricate to colliculate and lightly punctate, slightly wrinkled dorsomedially in some specimens; trochantellus  $0.4-0.8\times$  as dorsally long as broad;  $4^{th}$  tarsomere in female  $2.4-2.9\times$  as long as broad,  $2.6-3.1\times$  in male;  $5^{th}$  tarsomere of female  $2.9-3.2\times$  as long as broad, evenly broadened distally in dorsal view, nearly straight to moderately curved in lateral view;  $5^{th}$  tarsomere of male  $3.6-4.2\times$  as long as broad, subparallel-sided to evenly broadened distally in dorsal view, moderately curved in lateral view; hind outer pretarsal claws of female and male dimorphic, approximately as figured (Figs 2C, E). **Metasoma:** Fairly slender, not apically deep in female;  $T2$   $4.9-6.8\times$  as long as lateral height,

$3.8-6.8\times$  as long as dorsal width; thyridium narrowly oval to tear-shaped, midpoint positioned posterior of anterior margin of  $T2$  by  $0.3-0.4\times$  length of  $T2$ . Ovipositor short and straight or slightly upcurved,  $0.7-0.8\times$  length of  $T2$ .

**Color:** Generally orange to brownish-orange; face pale laterally and behind compound eyes; wings slightly to distinctly infumate; legs fairly evenly orange, apical tarsomeres slightly to distinctly darker; metasomal segments 4–8 (and in some specimens portions of 3) darker; setae of head and propodeum pale.

*Material examined.*—**Holotype:** female, Hawaii, **Kauai**, Na Pali-Kona Forest Reserve, Pihea Trail, elevation 4200 ft, 15 June 1982 (K. and E. Sattler) (BMNH). **Paratypes** (17 all from **Kauai**): 4 males, 1 female, same data as holotype; 1 male same data as holotype except collected 21 August 1982; 1 female, Na Pali-Kona Forest Reserve, Milolii ridge, elevation 3000 ft, 26 June 1982 (K. and E. Sattler) (BMNH); 1 male, 1 female, Na Pali-Kona Forest Reserve, Alakai Swamp Trail, elevation 3800 ft, June 1982 (K. and E. Sattler) (BMNH); 1 male, Kokee State Park, Kumuwela Ridge, Waininiua Trail, elevation 3800 ft, 24 June 1982, (K. and E. Sattler) (BMNH); 1 female, Kokee State Park, Kaluapuhi Trail, elevation 4000 ft, 9 June 1982, (K. and E. Sattler) (BMNH); 1 male, Alakai Swamp, Kelekua Hut, elevation 4520 ft, 1982 (K. and E. Sattler) (BMNH); 2 females, Kokee Camp, elevation 3600 ft (1 female 1 April 1961, 1 female 30 March 1961) (D. F. Hardwick) (CNCI); 2 females, 1 male, Na Pali-Kona Forest Reserve, Alakai Swamp at junction of Pihea Trail, elevation 1200 m, 18 August 2006, UV light trap, (D. Rubinoff and J. Eiben) (Manoa).

*Etymology.*—The species name is given in honor of the late Dr. James S. Ashe for his critical, constructive, and enthusiastic advice and support given to me which much improved this work.

### *Enicospilus bellator* Perkins

Fig. 9

*Enicospilus bellator* Perkins 1915: 528. Lectotype (designated by Townes et al. 1961: 270) female, Hawaii [Is.], Kilauea, VII.06, R.C.L. Perkins (BPBM) [examined]. Swezey and Brian 1927:

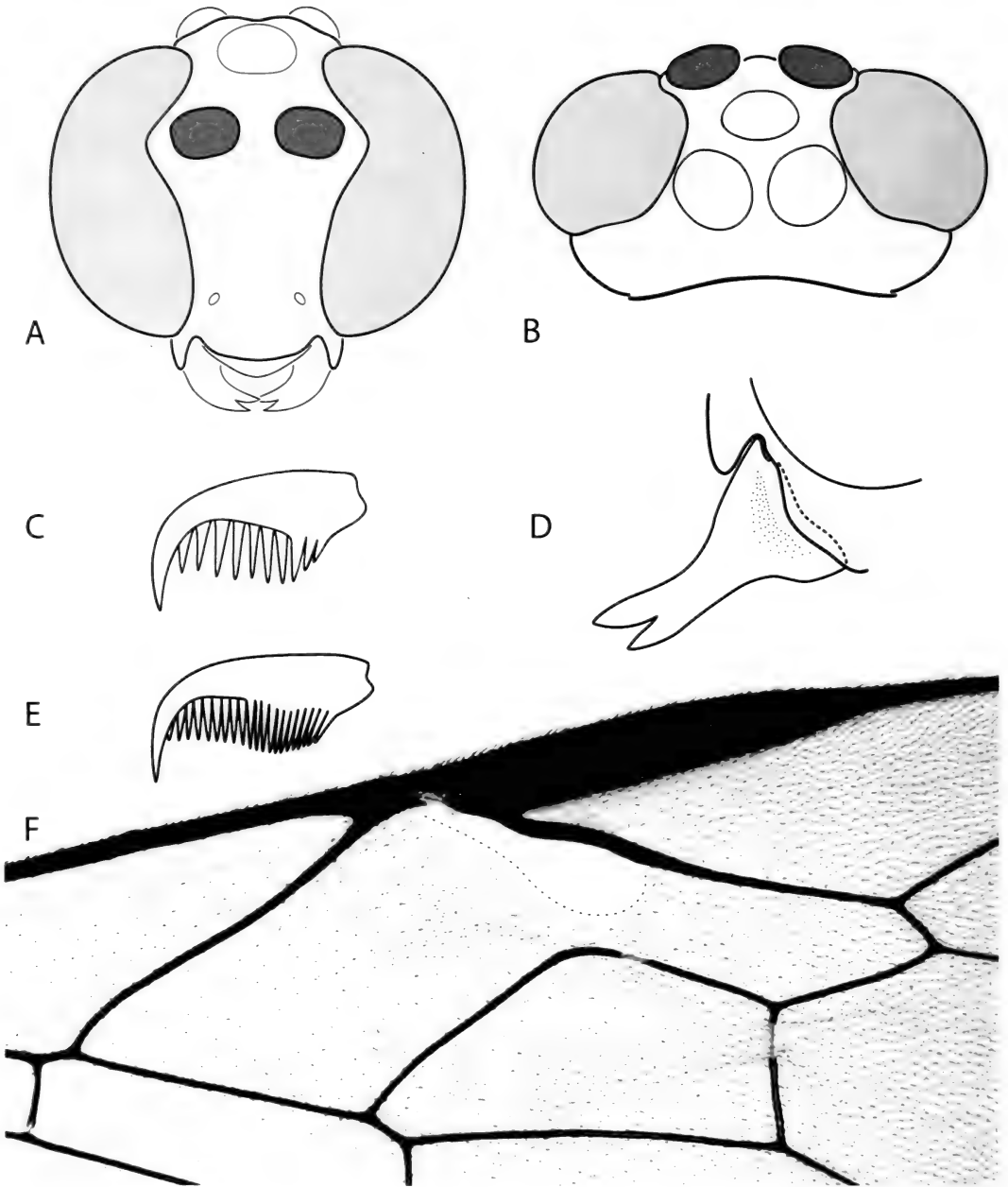


Fig. 2. *Enicospilus ashei*: A, frontal aspect of head; B, dorsal aspect of head; C, female hind outer claw; D, mandible; E, male hind outer claw; F, discosubmarginal cell of fore wing.

412. Townes et al. 1961: 270. Gupta 1987: 514.  
Yu and Horstmann 1997: 734.

*Enicospilus* (*Enicospilus*) *bellator* Perkins; Cushman 1944: 49.

*Remarks.*—This rarely collected species is similar to *E. castaneus* and *E. dispilus* in the

relatively flat and coarsely punctured dorsal part of the scutellum and the strongly curved, parallel-sided or basally swollen male pretarsal claw; it is distinguished from these species by the narrow fenestra lacking a distinct alar sclerite (Fig. 9). The few individuals I have seen have all been fairly

large (fore wing length 12.0–16.0 mm), red to reddish-brown, with the face and clypeus broadly yellow below the toruli outside the darker medial area; wings vary from hyaline to very slightly infumate.

***Enicospilus blackburni*, new name**

Fig. 10

*Enicospilus molokaiensis* Ashmead 1901: 349. Lectotype (designated by Townes et al. 1961: 282) female, Molokai, Mts, 4000 ft, 4.1893, Perkins (BMNH); preoccupied in *Enicospilus* by *E. molokaiensis* (Ashmead 1900) (transferred from *Pycnophion* to *Enicospilus* below). Perkins 1907a: 44. Perkins 1913: cx. Perkins 1915: 523. Fullaway and Giffard 1919: 51. Swezey and Bryan 1927: 412. Townes et al. 1961: 282. Gupta 1987: 555. Yu and Horstmann 1997: 745.

*Henicospilus molokaiensis* (Ashmead); Szépligeti 1905: 27.

*Enicospilus* (*Enicospilus*) *molokaiensis* Ashmead; Cushman 1944: 46.

**Remarks.**—This common species can be recognized by the combination of its coloration (reddish-brown to orange throughout, with usual exception of yellowish parts of the face, clypeus, and gena; wings vary from hyaline to very slightly infumate); fore wing with an angle in 1m-cu medially and very broad fenestra with a single, often attenuated, posteriorly positioned sclerite (Fig. 10); and the slender aedeagus. It is usually fairly small to medium-sized, with a fore wing length of about 9.5 mm; occasionally it is as small as 7.5 mm or as large as 12.6 mm.

**Etymology.**—The species epithet is dedicated to the minister naturalist Thomas Blackburn, the first European to collect Hawaiian ophionine wasps (as well as many other Hawaiian insects) and send them to specialists in London.

***Enicospilus castaneus* Ashmead**

Fig. 11

*Ophion nigricans* Cameron 1883: 193. Lectotype (designated by Perkins 1915: 521 [His usage of “type” is herein regarded as equivalent to a lectotype designation (ICZN 1999: Art.

74.5).]) male, Sandwich, Hawaii [probably meaning Hawaii Island] (BMNH); preoccupied by *Ophion nigricans* Ruthe 1859, replaced with *O. nigrirulus* by Dalla Torre 1901. Blackburn and Cameron 1886: 180; 1887: 241. Ashmead 1901: 341. Alfken 1904: 573.

*Enicospilus castaneus* Ashmead 1901: 349. Lectotype (designated by Townes et al. 1961: 272 [Their usage of “type” is herein regarded as equivalent to a lectotype designation (ICZN 1999: Art. 74.5).]) female, Molokai, Mts, 3000 ft, 9 [?].1893, Perkins (BMNH); synonymized with *O. nigricans* (Cameron) by Perkins 1915: 534. Swezey and Williams 1932: 182. Townes et al. 1961: 271. Gauld and Mitchell 1981: 8. Gupta 1987: 521. Yu and Horstmann 1997: 736.

*Ophion nigrirulus* Dalla Torre 1901: 196; synonymized with *E. castaneus* Ashmead by Perkins 1915: 534. Szépligeti 1905: 31. Fullaway 1957: 271 [Misidentification of *Leptophion* sp. from Fiji (according to Gauld and Mitchell 1981)].

*Henicospilus castaneus* (Ashmead); Szépligeti 1905: 27.

*Ophion nigrirulus* Morley 1912: 64; preoccupied by *Ophion nigrirulus* Dalla Torre 1901.

*Enicospilus* (*Enicospilus*) *castaneus* Ashmead; Cushman 1944: 48.

**Remarks.**—This common, medium-sized to large species (fore wing length 8.0–16.0 mm) is similar to *E. bellator* and *E. dispilus* in the relatively flat and coarsely punctured dorsal part of the scutellum and the strongly curved, parallel-sided or basally swollen male pretarsal claw. It is distinguished from these species by the longer malar space (especially in the male), less convex compound eye, shorter antenna (especially in the female), and the single, small alar sclerite (Fig. 11). Occasionally a second vestigial alar sclerite is present, and in such cases females can be difficult to distinguish from *E. dispilus* as some overlap occurs in the antenna length. Coloration is usually generally red to brownish-red (less commonly more or less brown), typically with exception of yellowish areas of the face, clypeus, and gena. Often the mesosoma is much darker throughout or in patches variously distrib-

uted on the pronotum, mesopleuron, scutellum, and propodeum; wings vary from hyaline to slightly infumate.

*Enicospilus debilis* (Perkins),  
combination reinstated  
Fig. 12

*Athyreodon hawaiiensis* Ashmead 1901: 343. Holotype (by monotypy) male, Hawaii [Is.], Ola'a, (lost); preoccupied in *Enicospilus* by *E. hawaiiensis* (Ashmead 1900). Szépligeti 1905: 32. Perkins 1910: 679.

*Abanchogastra debilis* Perkins 1902: 141. Lectotype (designated by Cushman 1944: 54, not Townes et al. 1961: 274 as claimed) female [metasoma absent], [Oahu], Honolulu Mts [published as "Ko'olau range"], XII-02 (BPBM) [examined]; synonymized with *A. hawaiiensis* (Ashmead) by Cushman 1944. Szépligeti 1905: 33. Gupta 1987: 506.

*Athyreodon debilis* (Perkins); Perkins 1910: 680. Swezey 1915: 106. Perkins 1913: cx [in reference to the "smaller *Athyreodon*," presumably meaning *A. debilis*]

*Abanchogastra hawaiiensis* (Ashmead); Cushman 1944: 53. Cushman 1947: 464. Gauld 1985: 168. Yu and Horstmann 1997: 730.

*Enicospilus debilis* (Ashmead); Townes 1945: 737. Townes et al. 1961: 274.

**Remarks.**—This rarely collected species can be easily recognized by the combination of its small size (fore wing length 6.3–9.0 mm); brown, red, or orange coloration (with frequent exception of yellow parts of the face, clypeus, and gena; wings are hyaline to slightly infumate); slender mandibular teeth; absence of a posterior transverse carina of the mesosternum medially; and the lack of both a fenestra and sclerite in the fore wing discosubmarginal cell (Fig. 12).

*Enicospilus dispilus* Perkins  
Fig. 13

*Enicospilus dispilus* Perkins 1902: 143. Holotype [Perkins' use of "the type" is herein regarded as the original holotype designation (ICZN 1999: Art. 73.1.1)] female, [Oahu], Honolulu Mts [published as "Ko'olau range"], 1500 ft, XII.15. [R.C.L.P. [Perkins] (BPBM) [exam-

ined]. Perkins 1907a: 44. Perkins 1910: 670. Perkins 1915: 528. Swezey 1915: 105. Anonymous 1917: 286. Anonymous 1924: 345. Townes et al. 1961: 274. Gupta 1987: 527. Yu and Horstmann 1997: 737.

*Enicospilus dispilus* variety *pallipes* Perkins 1902: 143. Type not designated. Synonymized by Cushman 1944.

*Henicospilus dispilus* (Perkins); Szépligeti 1905: 27. Morley 1912: 49.

*Enicospilus* (*Enicospilus*) *dispilus* Perkins; Cushman 1944: 49.

**Remarks.**—This common, medium-sized to large species (fore wing length 11.0–17.0 mm) is similar to *E. bellator* and *E. castaneus* in the relatively flat and coarsely punctured dorsal part of the scutellum and the strongly curved, parallel-sided or basally swollen male pretarsal claw. It is distinguished from these species by the discosubmarginal cell which has two (rarely three) sclerites (Fig. 13), and with respect to *E. castaneus*, eyes more convex and a shorter malar space (especially in the male). In coloration it ranges from orangish or reddish-brown to dark brown throughout (usually with exception of yellowish parts of the face, clypeus, and gena); wings vary from hyaline to infumate (typically slightly infumate).

*Enicospilus dorsolineatus*, new species  
Fig. 3A–C

**Diagnosis.**—This yellow to yellowish-brown species is easily recognized by the dorsomedial dark line on the mesoscutum and metasoma. Should additional material reveal color variation, it can further be distinguished by the very narrow gena (Fig. 3B) and long malar space (Fig. 3A).

**Description.**—Length of fore wing about 13.0 mm in female. **Head:** Mandible fairly slender, slightly to moderately twisted, basal ventral margin weakly concave; outer surface generally smooth, without a distinct basal concavity, sparsely setose along a weak diagonal groove; upper tooth 1.5× as long as lower tooth, about as wide as lower tooth at base. Labrum 0.3× as long

as broad, apical margin flat medially, rounded laterally or trapezoidal. Malar space  $0.4\text{--}0.5\times$  as long as basal mandibular width. Clypeus in profile flat to weakly convex, proximal margin weakly distinct from lower face; in frontal view  $1.3\text{--}1.4\times$  as broad as long, apical margin broadly flat and impressed medially, rounded laterally, finely colliculate or coriaceous. Lower face  $0.6\times$  as broad as long, very lightly and evenly punctate (punctuation not denser or coarse medially). Compound eye large, moderately convex, head width in frontal view  $1.0\text{--}1.1\times$  length (Fig. 3A). Gena with setae pale, declined forward; in dorsal view very narrow, strongly constricted behind compound eye (Fig. 3B); GOI =  $3.6\text{--}3.9$ . Ocelli large, posterior ocellus separated from compound eye by about  $0.1\times$  its diameter, FI =  $0.6$ . Occipital carina dorsally rounded, ventrally ending just short of hypostomal carina. Flagellum in female  $1.8\times$  length of fore wing, with 61 segments, mid segment  $2.2\times$  as long as broad. **Mesosoma:** Mesoscutum moderately rounded anteriorly in profile, forming an angle of about  $70^\circ$ ; notauli weak or vestigial. Scutellum compact, in dorsal view  $1.3\times$  as long as anterior width; upper surface convex, evenly and rather coarsely punctate (relative to mesoscutum); lateral carinae moderately weak, extending about  $4/5$  scutellar length; posterior declined by about  $40^\circ$  in profile, lightly striate. Mesopleuron rugulo-punctate/striate; scrobe set in distinct depression; speculum weakly apparent; mesopleural sulcus with weak transverse ridges; epicnemial carina strong, medioventrally complete. Mesosternum with distinct lateral longitudinal depression behind epicnemial carina; posterior transverse carina present medioventrally. Lower metapleuron weakly convex, rugose, rugulostriate or coarsely punctate. Propodeum in profile weakly convex; setae pale, upright, posteriorly directed; spiracle narrowly oval, anterior furrow fairly shallow, rugostriate; anterior area  $0.1\times$  total propodeal length; anterior transverse cari-

na weakly present medially; posterior transverse carina absent; spiracular area smooth medially, rugose laterally behind spiracle,  $0.2\text{--}0.3\times$  total propodeal length; posterior area rugostriate anteriorly, rugose posteriorly. Separation between propodeum and lower metapleuron indicated by a weak furrow only (not carinate). Fore wing (Fig. 3C) pterostigma with distal end narrowed abruptly; discosubmarginal cell with 1 moderately large, triangular sclerite, the distal corner of which is attenuated relative to other corners; fenestra semicircular, extending apically to at least midpoint of Rs+2r, posterior margin extending to about  $4/5$  the distance between Rs+2r and 1m-cu; Rs+2r much thickened in basal half and slightly sinuous; Rs+M nearly straight or slightly arched in basal half; 1m-cu strongly arched; AI =  $0.8$ ; CI =  $0.3\text{--}0.5$ ; ICI =  $0.7\text{--}0.8$ ; SDI =  $1.0\text{--}1.1$ ; cu-a positioned proximal of Rs+M by  $0\text{--}0.1$  length of cu-a; 1st subdiscal cell sparsely and evenly setose anteriorly and apically, lacking setae in at least proximal, ventral part. Hind wing with about 8 hamuli in distal set; 1<sup>st</sup> abscissa of Rs slightly concave proximally, 2<sup>nd</sup> abscissa straight; 2<sup>nd</sup> abscissa of Cu1 emerging much nearer 1A than M, CI =  $0.2\text{--}0.3$ . Fore leg tibia  $10.2\text{--}10.6\times$  as long as wide, without an array of subapical spines on outer surface. Mid leg with coxa evenly colliculate; inner tibial spur  $1.3\times$  as long as outer spur. Hind leg with coxa in lateral view  $2.0\text{--}2.1\times$  as long as deep; trochantellus dorsally  $0.2\times$  as long as broad; 4<sup>th</sup> tarsomere in female  $2.1\text{--}2.2\times$  as long as broad in dorsal view; 5<sup>th</sup> tarsomere of female in dorsal view evenly broadened distally,  $3.2\text{--}3.4\times$  as long as broad, in lateral view slightly curved; pretarsal claw of female long, with about 13 preapical teeth. **Metasoma:** Elongate; T2 in female  $6.7\times$  as long as lateral height,  $4.6\text{--}4.9\times$  as long dorsal width; thyridium tear-shaped, positioned posterior of anterior margin of T2 by  $0.3\text{--}0.4\times$  length of T2. Ovipositor short and straight, about  $0.4\times$  length of T2.

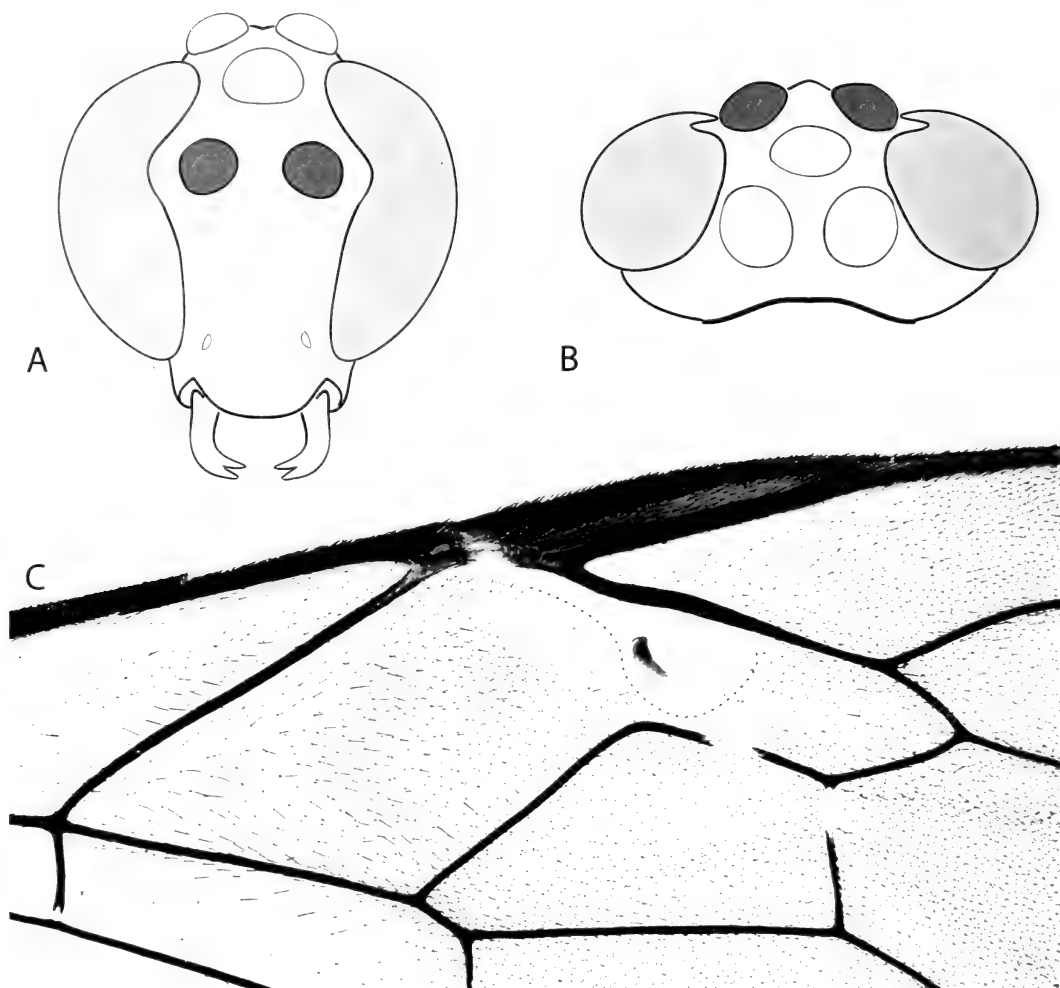


Fig. 3. *Enicospilus dorsolineatus*: A, frontal aspect of head; B, dorsal aspect of head; C, discal cell of fore wing.

**Color:** Generally brownish-yellow; head yellow throughout; mesoscutum with medial black stripe in anterior half; mesopleuron dark in specular area and broadly on mesosternum, anterior area of propodeal furrow with medial dark area; wings hyaline; legs brownish-yellow with apical tarsomeres darker; metasoma with dorso-medial black stripe on T3–T6 or T7.

**Material examined.**—**Holotype:** female, Hawaii, Hawaii Is.: Kilauea, October 1915, (W. M. Giffard) (BPBM). **Paratype:** female, same data as holotype except date 18 October 1916 (AEIC).

**Etymology.**—The species name is in reference to the dorsomedial stripe which is unique among Hawaiian Ophioninae.

*Enicospilus elefino*, new species  
Fig. 4A–E

**Diagnosis.**—The combination of the characteristics of the mandible, clypeus shape, compound eye, ocelli, gena, mesopleuron, mesopleural sulcus, mesocoxa, mesosternum, and thyridium serve to differentiate it from the only other small, black, stout *Enicospilus* species, *E. kauaiensis* and *E. vitreipennis*.



**Description.**—Length of fore wing 7.5–8.9 mm in male. **Head:** Mandible stout, slightly twisted; basal ventral margin very weakly concave; outer surface with strong basal concavity, generally smooth except for a few scattered light punctures and a small proximal area of coriaceous sculpture, sparsely setose, without diagonal groove; upper tooth 1.1–1.2× as long as lower tooth, wider than or about equal in width to lower tooth at base. Labrum 0.3× as long as broad, apical margin evenly rounded. Malar space 0.6–0.8× as long as basal mandibular width. Clypeus in profile weakly to moderately convex, proximal margin clearly distinct from lower face; in frontal view 1.7–1.8× as broad as long, evenly colliculate and lightly punctate, apical margin broadly rounded, blunt to fairly sharp, not impressed. Lower face 0.8–0.9× as broad as long, evenly colliculate and lightly punctate. Compound eye reduced, head width 1.2–1.3× length in frontal view (Fig. 4A). Gena with setae fairly long, declined forward; in dorsal view broadly rounded behind compound eye (Fig. 4B); GOI = 1.3–1.7. Ocelli small, lateral ocellus removed from compound eye by 1.3–1.4× its diameter; FI = 0.2; occipital carina dorsally flat, ventrally joining or ending well before hypostomal carina. Flagellum in male 1.0–1.2× fore wing length, with 40–41 long segments, mid segment 1.9–2.1× as long as broad. **Mesosoma:** Mesoscutum in profile rounded, anterior angle 80°–90°; notauli absent or weak. Scutellum compact and fairly narrow in dorsal view, 1.1–1.3× as long as anterior width; upper surface convex, evenly colliculate; lateral carinae fairly weak (at least posteriorly), convergent posteriorly, extending about 3/4 or more scutellar length; posterior gradually declined, in profile forming an angle of 35°–45°. Mesopleuron evenly colliculate throughout; scrobe distinct; speculum not apparent; mesopleural sulcus strong, with stout ridges; epicnemial carina fairly weak, in one examined specimen evanescent at

posterior ventral corner, narrowly absent to evanescent medioventrally. Mesosternum with distinct lateral longitudinal depression behind lateroventral corner of epicnemial carina; posterior transverse carina broadly absent medially by about 1/2 mesosternal width. Lower metapleuron moderately or strongly convex, evenly colliculate. Propodeum compact, convex in profile, moderately setose with erect (not declined posteriorly), apically curved (in an anterior direction) setae, at least posteriorly; spiracle very narrow, in one specimen examined nearly occluded by semicircular or triangular extension of its anterior margin; anterior furrow strong, rugose, anterior area 0.1–0.2× total propodeal length; anterior transverse and posterior transverse carinae absent; spiracular area evenly colliculate; posterior area evenly colliculate medially, becoming rugostriate posteriorly. Separation between propodeum and lower metapleuron indicated by a moderate groove (at least medially) but without carina. Fore wing (Fig. 4C) with pterostigma long and fairly slender, apically abruptly tapered; discosubmarginal cell narrow, without sclerites, fenestra ill-defined as narrow area of reduced pubescence; Rs+2r slender and straight; Rs+M sinuous; 1m-cu evenly arched in basal half; AI = 0.8–0.9; CI = 0.3; ICI = 0.5–0.8; SDI = 1.2–1.4; cu-a anterior of Rs+M by 0.5–0.6 length of cu-a; 1st subdiscal cell very sparsely setose, less-so proximally. Hind wing with about 7 hamuli in distal set; 1<sup>st</sup> abscissa of Rs basally concave, 2<sup>nd</sup> abscissa straight; 2<sup>nd</sup> abscissa of Cu1 positioned just posterior of midpoint between M and 1A, convex, CI = 0.4. Fore leg with tibia compact, 5.5–6.0× as long as wide; fairly weak subapical spines scattered on anterior surface. Mid leg with distinct transverse stout ridges on dorsomedial surface of coxa; inner tibial spur 1.3× as long as outer spur. Hind leg with coxa in lateral view 1.6× as long as wide, evenly colliculate; trochantellus in lateral view 0.1–0.2× as dorsally long as broad; 4<sup>th</sup> tarsomere of

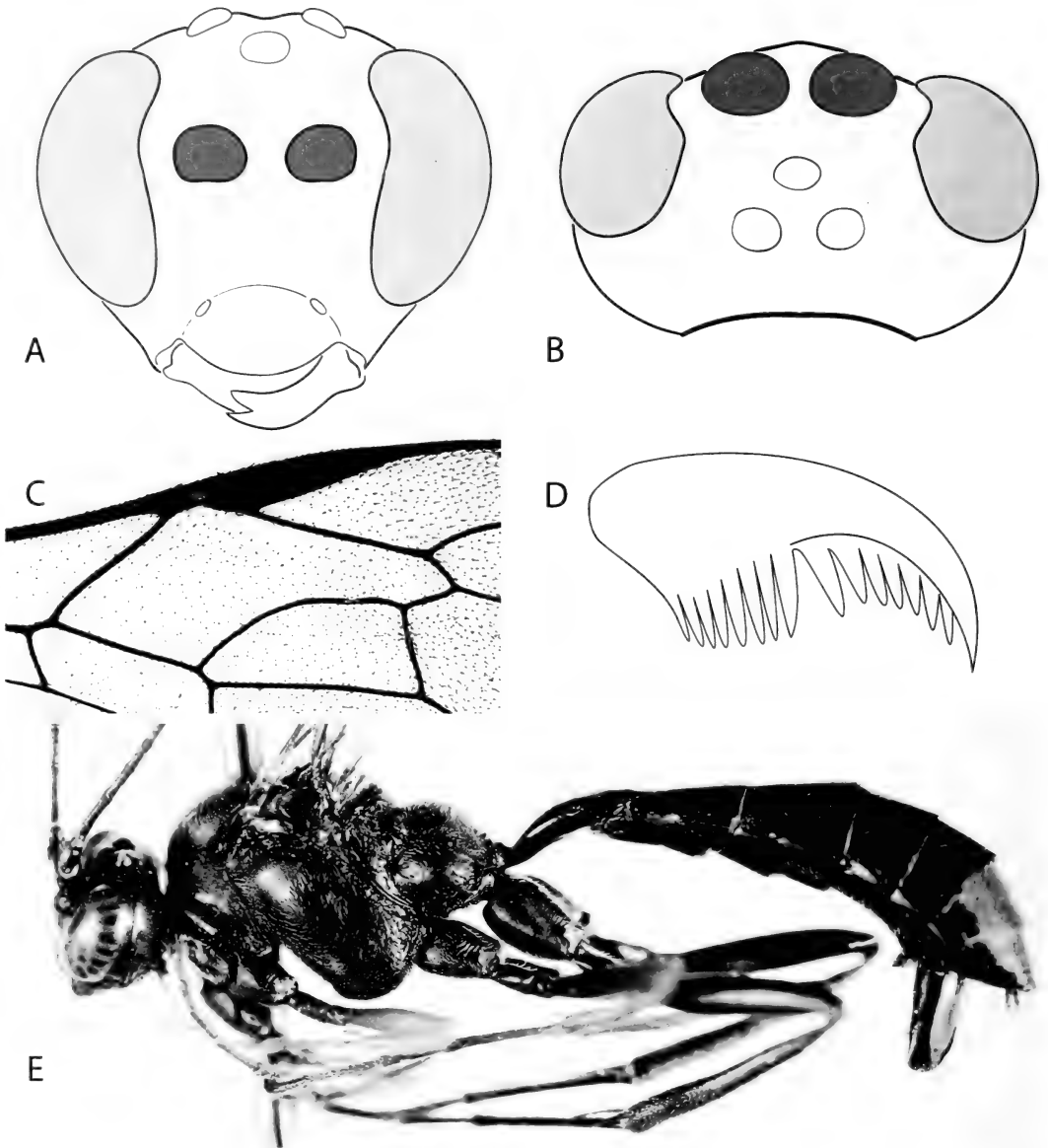


Fig. 4. *Enicospilus elekino*: A, frontal aspect of head; B, dorsal aspect of head; C, discosubmarginal cell of fore wing; D, male hind outer claw; E, lateral aspect of body.

male  $1.4\text{--}1.8\times$  as long as broad in dorsal view; apical tarsomere of male  $2.6\times$  as long as broad in dorsal view, straight in lateral view; hind outer pretarsal claw of male with teeth densely pectinate at least basally, teeth distributed evenly or divided once or more by a conspicuous space (Fig. 4D). **Metasoma** fairly narrow and slender in lateral view yet dorsally rather broad (Fig. 4E); T2  $1.2\text{--}1.5\times$  as long as lateral height,  $1.3\text{--}1.5\times$

as long as dorsal width; thyridium reduced, positioned posterior of anterior margin of T2 by  $0\text{--}0.1\times$  the length of T2.

**Color:** Generally black except femur, tibia, and tarsus of fore leg and tibia and tarsus of mid leg brown; wings slightly to distinctly infumate; setae of head with brown tint, that of propodeum pale.

**Remarks.**—The female of this species is unknown. Its discovery would be interesting

given its similarity to both *E. kauaiensis*, a species with a long, upcurved ovipositor, and *E. vitreipennis*, which has a short, straight ovipositor. Chances for its discovery may be good given that it was taken as recently as 1984 in a protected accessible area of Maui.

*Material examined*.—**Holotype**: Male, Hawaii, **Maui**, Haleakala, Makawao Forest Reserve, elevation 5700 ft, 17 June 1975 (R. Burckhart), "sweeping" (BPBM). **Paratype**: male, **Maui**, Haleakala, West slope, elevation 5500 ft, 4 June 1984 (A. C. Medeiros), on *D. plantaginea*.

*Etymology*.—The species name is a composite of the Hawaiian words *ele* and *kino* meaning "black" and "body," respectively. It is treated as a noun in apposition.

*Enicospilus ferrugineus* (Perkins),  
reinstated combination  
cf. Fig. 15

*Pleuroneurophion ferrugineus* Perkins 1915: 533.

Lectotype (designated by Townes et al. 1961: 274 [Their usage of "type" is herein regarded as equivalent to a lectotype designation (ICZN 1999: Art. 74.5).]) female, Maui, Haleakala, 2000 ft, R.C.L.P. [Perkins] (BPBM) [examined]; synonymized with *Enicospilus debilis* (Perkins) by Townes et al. 1961: 274; reinstated in *Enicospilus* by Townes and Townes 1973; synonymized with *Abanchogastra hawaiiensis* Ashmead by Yu and Horstmann 1997: 730.

*Enicospilus* (*Pleuroneurophion*) *ferrugineus* (Perkins); Cushman 1944: 46.

*Enicospilus ferrugineus* (Perkins); Townes and Townes 1973: 371. Gupta 1987: 532.

*Remarks*.—The species status of this nomen is dubious, though it is not near *Enicospilus debilis* (Perkins) with which it was once synonymized (see above). Other than differences in color and distribution listed in the key, it is virtually identical to *E. hawaiiensis* (Ashmead). As long as both of these differences hold, an argument can be made for its continued recognition.

*Enicospilus fullawayi* Cushman  
Fig. 14

*Enicospilus* (*Eremotyloides*) *fullawayi* Cushman 1944: 45. Holotype (by monotypy and origi-

nal designation) female, Kauai, Halemanu, 8 June 1919, H. T. Osborn (USNM, #56661). Cushman 1947: 473.

*Enicospilus fullawayi* Cushman; Townes et al. 1961: 276. Gupta 1987: 536.

*Remarks*.—This rarely collected, medium-sized species (fore wing length 8.2–9.8 mm) can be recognized by its extremely slender metasoma (dorsomedial length of exposed portion of T5 in female, T4 in male, greater than lateral depth) combined with the broad fenestra containing a single, linear, posteriorly positioned sclerite (Fig. 14). Each of the relatively few known specimens is dark brown with frequent exception of yellow or whitish parts of the face, clypeus, and gena; the wings vary from hyaline to slightly infumate.

*Enicospilus gladiator*, new species  
Fig. 5A–D

*Diagnosis*.—This species is easily recognized by the combination of an angulate 1m-cu vein with a short stub and two alar sclerites (the second may be translucent, it does not show in the figure), the proximal one medially positioned between veins Rs+2r and 1m-cu (Fig. 5C).

*Description*.—Length of fore wing 8.6–11.0 mm in female, 6.7–9.3 mm in male. **Head**: Mandible moderately slender, weakly twisted; basal ventral margin weakly to moderately concave; outer surface without strong basal concavity, sparsely to moderately setose with hairs fairly long and scattered, without diagonal groove; upper tooth long, 1.3–1.5× as long as lower tooth, about as wide as lower tooth at base. Labrum 0.2–0.3× as long as broad, apical margin broadly rounded to flat medially, appearing semicircular, triangular, or trapezoidal. Malar space 0.2–0.4× as long as basal mandibular width. Clypeus in profile moderately convex to more or less flat, proximal margin moderately to weakly distinct from lower face; in frontal view 1.7–1.9× as broad as long, apical margin broadly rounded to flat, sharp, weakly to

moderately impressed medially, lightly punctate and minutely to moderately colliculate. Lower face  $0.7\text{--}0.8\times$  as broad as long, lightly punctate and/or colliculate (more strongly so medially in some specimens examined). Compound eye large and strongly convex, head width in frontal view  $1.2\text{--}1.3\times$  length (Fig. 5A). Gena with setae short, inconspicuous and declined forward; in dorsal view slightly to moderately rounded behind compound eyes (Fig. 5B);  $\text{GOI} = 1.9\text{--}2.8$ . Ocelli large, posterior ocellus touching compound eye or separated by about  $0.1\times$  its diameter,  $\text{FI} = 0.5\text{--}0.6$ . Occipital carina dorsally rounded, ventrally joining hypostomal carina. Flagellum in female about  $1.2\times$  length of fore wing, with 41–45 segments, mid segment  $1.7\text{--}2.1\times$  as long as broad; in male  $1.4\text{--}1.6\times$  length of fore wing, with 44–47 segments, mid segment  $1.9\text{--}2.1\times$  as long as broad. **Mesosoma:** Mesoscutum strongly rounded anteriorly in profile, anterior angle  $75\text{--}90^\circ$ ; notauli distinct or indistinct. Scutellum in dorsal view  $1.1\text{--}1.4\times$  as long as anterior width; upper surface weakly convex to nearly flat, colliculate, with or without minute transverse striations; lateral carinae moderately to strongly convergent, extending  $4/5$  or more scutellar length; posterior declined by about  $30^\circ$  in profile. Mesopleuron with fine irregularly transverse striations (common) or evenly colliculate throughout (one examined specimen), scrobe small but distinct; set in shallow groove which may extend dorsally toward subalar prominence and define a speculum (not evident in some individuals, in these the relief of mesopleuron being rather even); mesopleural sulcus with fine to moderately stout transverse ridges; epicnemial carina strong, complete medioventrally. Mesosternum without lateral longitudinal depression; with posterior transverse carina present medioventrally. Lower metapleuron weakly to moderately convex, evenly colliculate to irregularly striate. Propodeum in profile rounded anteriorly, flat medially and posteriorly (in female at least, somewhat more

shallowly rounded to flat throughout in some males examined); moderately setose with setae posteriorly declined; spiracle narrow; anterior furrow strong, rugulose to irregularly striate, anterior area  $0.1\text{--}0.2\times$  total propodeal length; anterior transverse carina present or absent, posterior transverse carina absent; spiracular area evenly colliculate,  $0.2\text{--}0.3\times$  total propodeal length; posterior area rugulose to finely areolate, becoming weakly striate medially in some individuals. Separation between propodeum and lower metapleuron variously indicated by carina and/or by a furrow, each of which may be fully or in part absent. Fore wing (Fig. 5C) with pterostigma long, narrowed rather abruptly distally; discosubmarginal cell with 2 sclerites, the basal one large and semicircular, positioned medially within fenestra, many examined specimens with a ventral, linear extension, distal sclerite transversely linear, faint (not visible in figure), outlining distal margin of fenestra as well as ventral margin in some individuals, fenestra fairly long and broad, apical margin extending to about midpoint of  $\text{Rs}+2\text{r}$ , posterior margin extending to near  $1\text{m-cu}$ ;  $\text{Rs}+2\text{r}$  thickened and sinuous in basal half;  $\text{Rs}+\text{M}$  straight or slightly arched in basal half;  $1\text{m-cu}$  angulate medially with short knob-like stub;  $\text{AI} = 0.9\text{--}1.9$ ;  $\text{CI} = 0.5\text{--}0.6$ ;  $\text{ICI} = 0.4\text{--}0.6$ ;  $\text{SDI} = 1.0\text{--}1.3$ ;  $\text{cu-a}$  anterior of  $\text{Rs}+\text{M}$  by  $0\text{--}0.4$  length  $\text{cu-a}$ ; 1st subdiscal cell with a few scattered setae apically and/or medially. Hind wing with 1<sup>st</sup> abscissa of  $\text{Rs}$  slightly concave or straight basally, 2<sup>nd</sup> abscissa nearly straight; 2<sup>nd</sup> abscissa of  $\text{Cu1}$  emerging much nearer  $1\text{A}$  than  $\text{M}$ ,  $\text{CI} = 0.2\text{--}0.3$ . Fore leg tibia  $8.5\text{--}10.0\times$  as long as wide, without an array of subapical spines on outer surface. Mid leg with coxa evenly colliculate which may become minutely wrinkled dorsomedially; inner tibial spur  $1.2\text{--}1.4\times$  as long as outer spur. Hind leg with coxa in lateral view  $1.7\text{--}2.0\times$  as long as deep; trochantellus dorsally  $0.5\text{--}0.8\times$  as long as broad; 4<sup>th</sup> tarsomere in female  $2.7\text{--}2.8\times$  as long as broad in dorsal view,  $2.7\text{--}3.2\times$  in male; 5<sup>th</sup> tarsomere of

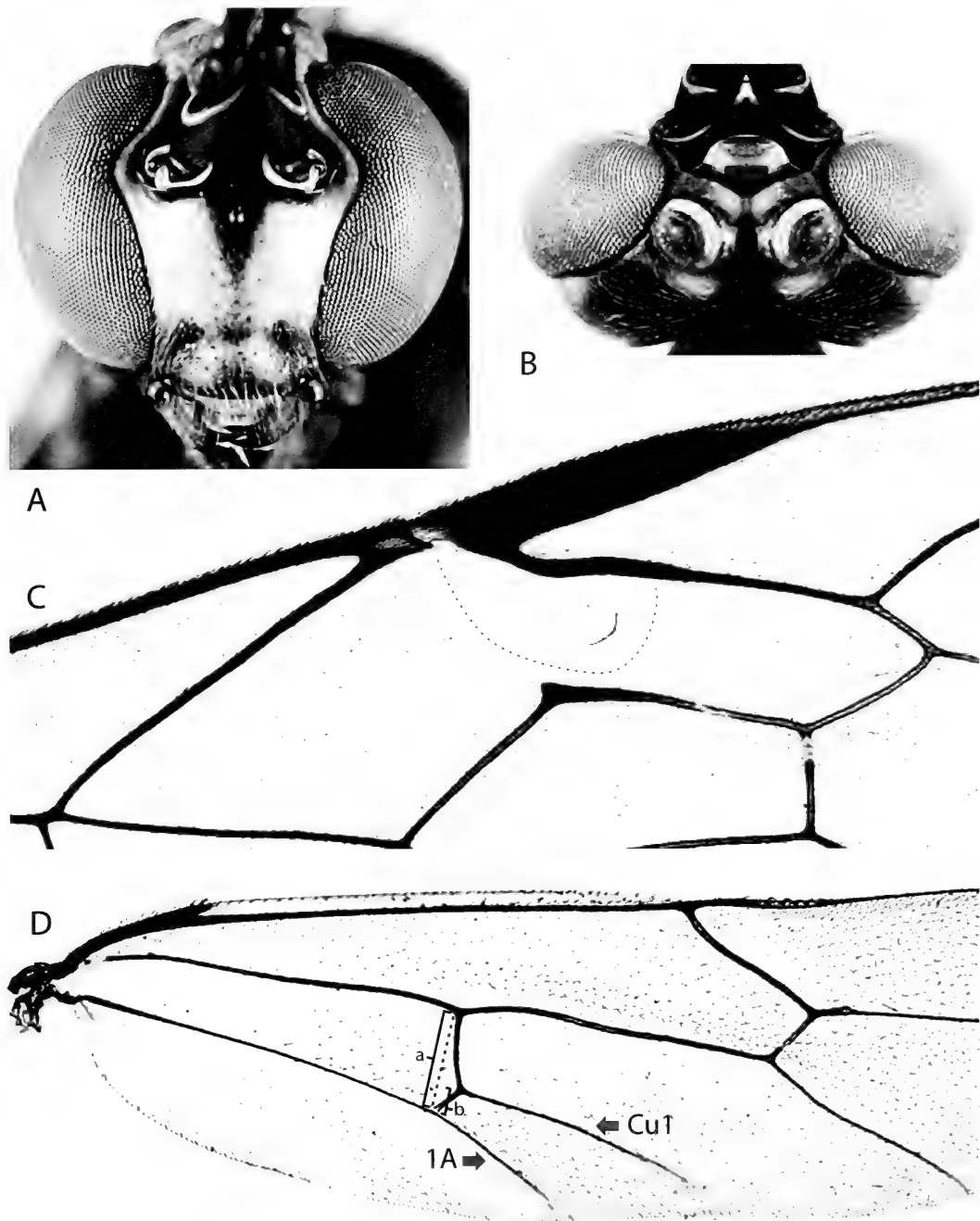


Fig. 5. *Enicospilus gladiator*: A, frontal aspect of head; B, dorsal aspect of head; C, discosubmarginal cell of fore wing; D, hind wing, cubital index = ratio of b to a.

female in dorsal view evenly broadened distally, 3.0–3.1× as long as broad, in lateral view nearly straight; 5<sup>th</sup> tarsomere of male in dorsal view somewhat abruptly widened

apically, 3.4–3.6× as long as broad, in lateral view nearly straight or slightly curved; pretarsal claw of female evenly curved, with 7–10 pre-apical teeth (cf. Fig. 6C);

pretarsal claws of male longer and densely pectinate (cf. Fig. 6D). **Metasoma:** Fairly compact and apically deep in female; T2 in female  $4.8\text{--}5.7\times$  as long as lateral height,  $2.7\text{--}3.6\times$  as long as dorsal width; T2 in male  $5.2\text{--}8.9\times$  as long as lateral height,  $4.3\text{--}6.2\times$  as long as dorsal width; thyridium tear-shaped to elliptical, positioned posterior of anterior margin of T2 by  $0.3\text{--}0.4\times$  length of T2. Ovipositor long and straight, about  $2.0\times$  length of T2, with slight swelling distal of midpoint.

**Color:** Generally evenly brown to brownish-red throughout, paler on face, behind compound eyes and, in some individuals, variously light brown on anterior pronotum, notaulus, subalar prominence, mesepimeron, and distal leg podites (other than apical tarsomeres and pretarsus which are dark); wings hyaline to slightly infumate; setae white to pale brown.

*Material examined.*—**Holotype:** female, Hawaii, **Kauai:** Kokee State Park, near main entrance,  $22.1194^\circ$ ,  $-159.6670^\circ$ , 1084 m elevation, 27–28 May 2006, UV light trap (D. J. Bennett) (BPBM). **Paratypes** (13, all from **Kauai**): 1 male, Kokee Camp, 3600 ft elevation, 29 March 1961 (D. F. Hardwick) (CNCI); 1 female, Kokee, 3400 ft elevation, 16 August 1961 (G. and J. Holland) (CNCI); 1 male, Na Pali-Kona Forest Reserve, Milolii Ridge, 3000 ft elevation, 26 June 1982 (K. and E. Sattler) (BMNH); 1 female, Kokee State Park, Kaluapuhi Trail, about 5 miles from lower trailhead, approximately  $22.1432^\circ$ ,  $-159.6421^\circ$ , 1150 m elevation, 28–29 May 2006, UV light trap (D. J. Bennett) (BPBM); 2 females, Kokee Road, 4000 ft elevation, 19 May 1982 (J. W. Beardsley) (BPBM); 1 female, Kumuwela, 8 August 1921, (Swezey) (BPBM); 2 males, Nualolo Valley, 3400 ft elevation, August 1952 (D. E. Hardy) (BPBM); 1 male, Kokee, 13–17 September 1965 (BPBM); 2 females, Kokee State Park, Discovery Center, 28 May 1998 (M. J. and C. A. Tauber) (BPBM); 1 female, Kokee, 4–6 August 1961 (Maa, Miyatake, and Shimoto) (BPBM).

*Etymology.*—The species epithet, a Latin noun for “long, slender,” is in reference to the long, straight ovipositor characteristic of this species.

### *Enicospilus hainesi*, new species

Fig. 6A–E

*Diagnosis.*—The long, broad fenestra lacking alar sclerites is unique among Hawaiian Ophioninae (Fig. 6E). Also helpful in recognizing this species is the shape of 1m-cu and the long, straight ovipositor.

*Description.*—Length of fore wing  $7.4\text{--}9.4$  mm in female,  $6.6\text{--}8.7$  mm in male. **Head:** Mandible moderately slender to moderately stout, evenly or somewhat abruptly tapered proximally, slightly twisted; basal ventral margin at least slightly concave; outer surface with setae scattered or loosely aggregated medially, without diagonal groove, basal concavity shallow; upper tooth long,  $1.2\text{--}1.5\times$  as long as lower tooth, about equal in width to lower tooth or the latter slightly wider at base. Labrum  $0.2\text{--}0.3\times$  as long as broad, apical margin broadly rounded. Malar space  $0.3\text{--}0.5\times$  as long as basal mandibular width. Clypeus in profile weakly to moderately convex, weakly to moderately distinct from lower face; in frontal view  $1.6\text{--}2.0\times$  as broad as long, coriaceous to colliculate, sparsely and lightly punctate, apical margin sharp, broadly flat, weakly to distinctly impressed medially. Lower face  $0.7\text{--}0.8\times$  as broad as long, lightly punctate and coriaceous to colliculate. Compound eye large and strongly convex, head width in frontal view  $1.2\text{--}1.3\times$  length (Fig. 6A). Gena with setae short, inconspicuous and declined forward; in dorsal view moderately rounded behind compound eye (Fig. 6B); GOI =  $2.2\text{--}3.1$ . Ocelli large, lateral ocellus removed from compound eye by  $0.1\text{--}0.2\times$  its diameter; FI =  $0.4\text{--}0.6$ . Occipital carina dorsally flat or broadly rounded, ventrally joining hypostomal carina. Flagellum in female  $1.3\text{--}1.5\times$  length of fore wing, with 44–45 segments, mid segment  $1.9\text{--}2.3\times$  as long as broad; in male  $1.5\text{--}1.6\times$  length of fore wing, with 45–51 segments, mid segment  $2.0\text{--}2.2\times$  as long as broad. **Mesosoma:** Mesoscutum strongly rounded in profile, anterior angle  $70^\circ\text{--}80^\circ$ ; notauli



weak to distinct. Scutellum in dorsal view  $1.2\text{--}1.4\times$  as long as anteriorly broad, with upper surface more or less flat to weakly convex, colliculate; lateral carinae moderately weak to moderately strong, moderately convergent, extending near entire scutellar length, albeit weakly so posteriorly; posterior declivity angled by  $30^\circ\text{--}45^\circ$ , striate, nearly smooth or colliculate. Mesopleuron colliculate and transversely rugulostriate; scrobe distinct or indistinct; speculum distinct or indistinct; mesopleural sulcus with weak transverse ridges; epicnemial carina strong, complete medioventrally. Mesosternum with or without shallow depression behind lateroventral corner of epicnemial carina; with posterior transverse carina complete medioventrally. Lower metapleuron moderately convex, colliculate and/or rugulose. Propodeum in profile weakly convex; with setae low-lying and posteriorly declined; anterior furrow strong, rugostriate, anterior area about  $0.1\times$  total propodeal length; anterior transverse carina in female strong, extending laterally almost to lower metapleuron, in male narrowly present as a weak medial vestige; posterior transverse carina absent; spiracular area smoothly colliculate,  $0.2\text{--}0.3\times$  total propodeal length; posterior area rugose becoming areolate in part posteriorly in some individuals. Separation between propodeum and metapleuron indicated by a weak furrow posteriorly and a distinct, evanescent, or irregular carina anteriorly. Fore wing (Fig. 6E) with pterostigma long, extending about  $3/4$  the length of Rs+2r, fairly abruptly narrowed distally; discosubmarginal cell without sclerites (vestiges apparent in some individuals), fenestra moderately long and broad, extending apically to  $2/3\text{--}3/4$  the length of Rs+2r and posteriorly to near 1m-cu; Rs+2r thickened medially, at least slightly arched (rather than sinuous); Rs+M slightly to distinctly arched, at least basally; 1m-cu strongly angulate medially with a distinct swelling or short stub projected anteroproximally; AI =  $1.5\text{--}2.6$ ;

CI =  $0.3\text{--}0.5$ ; ICI =  $0.2\text{--}0.3$ ; SDI =  $1.0\text{--}1.1$ ; cu-a anterior of Rs+M by  $0.3\text{--}0.5$  length of cu-a; 1<sup>st</sup> subdiscal cell sparsely and evenly pubescent or nearly devoid of setae throughout. Hind wing with 5–6 hamuli in distal set; 1<sup>st</sup> abscissa of Rs slightly concave basally or sinuous, 2<sup>nd</sup> abscissa more or less straight; 2<sup>nd</sup> abscissa of Cu1 positioned well below midpoint between M and 1A, CI =  $0.2\text{--}0.4$ . Fore leg with tibia  $7.4\text{--}9.1\times$  as long as wide, subapical spines absent or present as few and weak. Mid leg with coxa colliculate, becoming slightly rugulose dorsoposteriorly; inner tibial spur  $1.2\text{--}1.4\times$  as long as outer spur. Hind leg with coxa in lateral view  $1.5\text{--}1.8\times$  as long as deep, colliculate and at least slightly rugulose dorsoposteriorly; trochantellus  $0.4\text{--}0.6\times$  as dorsally long as broad; 4<sup>th</sup> tarsomere of female  $2.2\text{--}2.7\times$  as long as broad,  $2.4\text{--}2.9\times$  in male; 5<sup>th</sup> tarsomere of female  $2.4\text{--}2.9\times$  as long as broad, evenly broadened apically in dorsal view, nearly straight to slightly curved in lateral view; 5<sup>th</sup> tarsomere of male  $3.1\text{--}3.3\times$  as long as broad, evenly broadened apically in dorsal view, in lateral view moderately curved; pretarsal claw of female and male approximately as figured (Fig. 6C, D). **Metasoma:** Apically deep in female; T2  $4.3\text{--}5.3\times$  as long as lateral height,  $2.8\text{--}4.2\times$  as long as dorsal width; thyridium narrowly oval to tear-shaped, midpoint positioned posterior of anterior margin of T2 by  $0.3\text{--}0.4\times$  length of T2. Ovipositor long and straight, about  $2.1\times$  length of T2.

**Color:** Generally brown or reddish-brown; head lighter brown except variously darker on clypeus, face medially, frons, and posterior gena; wings hyaline to slightly infumate; legs slightly lighter than body except coxae (and in some individuals additional basal podites); setae white to pale brown.

**Remarks.**—This species is only known from rather recently collected material taken from within and near Honolulu. Despite the suspicious locality data (one such location is a Honolulu Pier), it is an obvious native Hawaiian insect, sharing

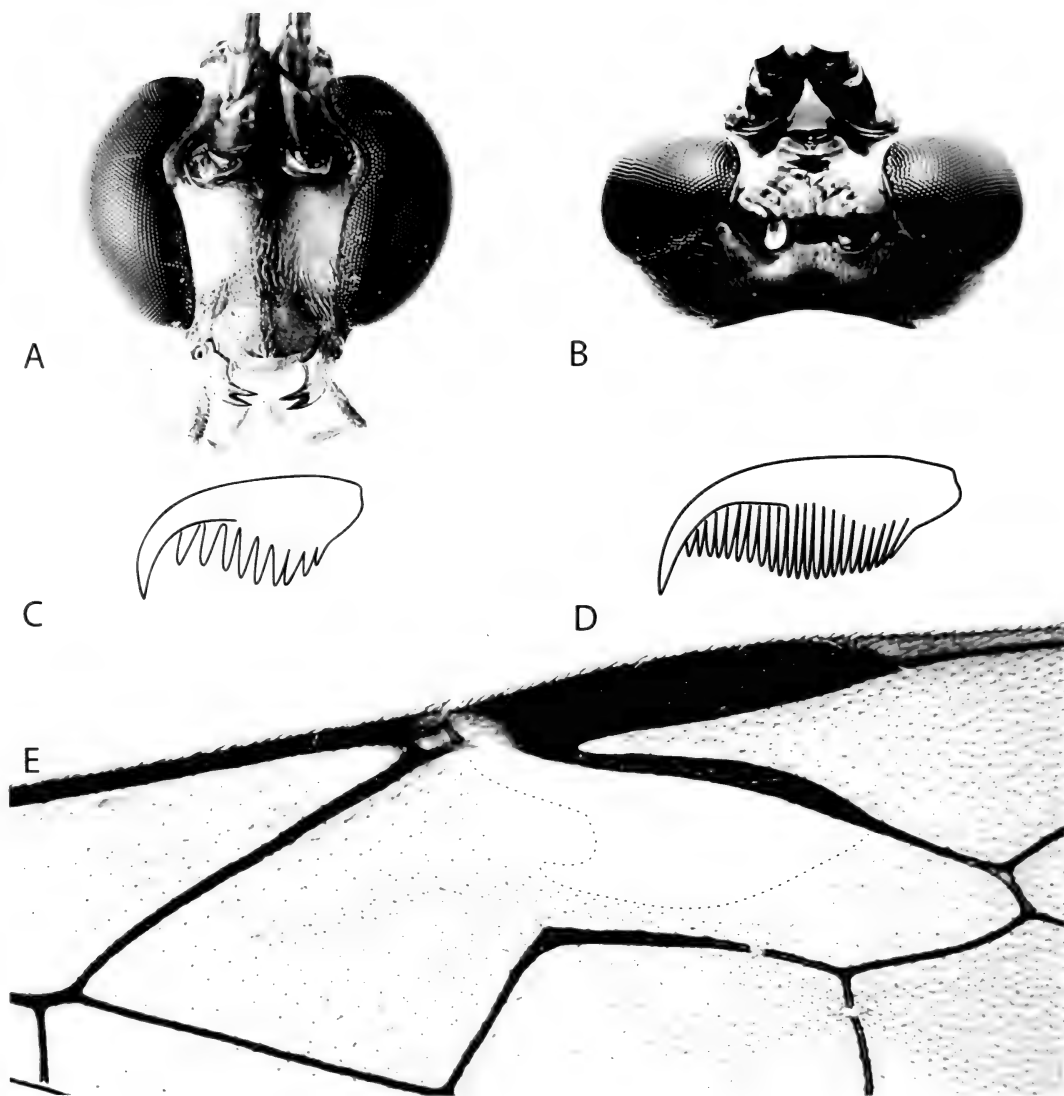


Fig. 6. *Enicospilus hainesi*: A, frontal aspect of head; B, dorsal aspect of head; C, male hind outer claw; D, female hind outer claw; E, discosubmarginal cell of fore wing.

typical general features of Hawaiian *Enicospilus* (colliculate punctation and lack of fore-tibial spines) and further resembles particular Hawaiian species such as *E. kaalae* (fenestra shape) and *E. hawaiiensis* (long, straight ovipositor). It is peculiar that it was never found by the early, prolific Hawaiian entomologists such as Perkins and Swezey who collected heavily in areas such as Tantalus where it occurs. The late Hymenopterist Dr. John Beardsley realized this conundrum and left a note on a specimen in

the BPBM postulating a switch to a non-native host as a possible explanation (one label even reads "Manoa vegetable garden"). Presumably under this scenario it was formerly rare and escaped capture but is more common now owing to this change. Discovery of the host range of this species both within Honolulu and its surrounding forests could be of potential general interest.

*Material examined*.—**Holotype**: female, Hawaii, Oahu, Mt. Tantalus, elevation 1900 ft, 20

September 1985 (W. E. Perreira) (BPBM). **Paratypes** (12 all from **Oahu**): 1 female, Poamoho Trail summit, elevation 2500 ft, 5 May 1995 (A. Asquith) (BPBM); 1 female, 1 male, Manoa, 4 October 1984, "vegetable garden," (K. Rhoads) (BPBM); 1 female, Ko'olau Mts, Wiliwilinui Trail, 6 June 2006, UV light trap (J. Eiben and W. Haines) (Manoa); 2 females, 3 males, Waianae Mts, Honouliuli Preserve, Palikea Trail, elevation 2700 ft, 15–16 May 2006, UV light trap (W. Haines) (Manoa); 1 male, Honolulu, Pier 32, 28 November 1978, light trap (Beardsley) (BPBM); 1 female, 1 male, Kaluaa Gulch, 18 November 1984, (Perlman) (BMBP).

**Etymology.**—This species is dedicated to the Lepidopterist Will Haines who collected the majority of specimens known of this species.

***Enicospilus hawaiiensis* (Ashmead)**

Fig. 15

*Pleuroneurophion hawaiiensis* Ashmead 1900: 86. Holotype (by monotypy) female, Hawaii [presumably Hawaii Island], Koebele [Coll.] (USNM, #5553); transferred to *Enicospilus* by Cushman 1944. Ashmead 1901: 342.

*Enicospilus* (*Pleuroneurophion*) *hawaiiensis* (Ashmead); Cushman 1944: 46.

*Enicospilus hawaiiensis* [! ] (Ashmead); Townes 1945: 737. Townes 1957: 116. Yu and Horstmann 1997: 741.

*Enicospilus hawaiiensis* (Ashmead); Cushman 1947: 466. Townes et al. 1961: 277. Gupta 1987: 539.

**Remarks.**—This small to medium-sized species (fore wing length 8.5–13.0 mm) can be recognized by the combination of its long, straight ovipositor; 1m-cu of fore wing with a medial stub (Fig. 15); discosubmarginal cell without a sclerite; and brown to slightly reddish-brown coloration (with typical exception of yellowish areas of the face, clypeus and gena; wings are hyaline or very slightly infumate).

***Enicospilus kaalae* Ashmead**

Fig. 16

*Enicospilus kaalae* Ashmead 1901: 347. Lectotype (designated by Townes et al. 1961: 278 [Perkins' (1910: 678) claim that the type of

this species is from Kauai is not herein regarded as a valid lectotype designation as it does not refer to an individual from Ashmead's syntype set as published.]) male, Oahu, Ka'ala Mts, 6500 ft (USNM). Perkins 1910: 278. Perkins 1913: cix. Perkins 1915: 524. Anonymous 1955: 386. Townes et al. 1961: 278. Gupta 1987: 545. Yu and Horstmann 1997: 742.

*Enicospilus semirufus* Perkins 1902: 142. Lectotype (designated by Townes et al. 1961: 278 [Their usage of "type" is herein regarded as equivalent to a lectotype designation (ICZN 1999: Art. 74.5).]) female, Oahu, Honolulu Mts [published as Ko'olau range] (BPBM) [examined]; synonymized by Perkins 1910.

*Henicospilus kaalae* (Ashmead); Szépligeti 1905: 27.

*Henicospilus semirufus* (Perkins); Szépligeti 1905: 27. Morley 1912: 52.

*Enicospilus* (*Enicospilus*) *kaalae* Ashmead; Cushman 1944: 47.

**Remarks.**—This large (fore wing length 12.5–17.5 mm) and common species (particularly on Kauai) is consistently colored dark brown to black on the mesosoma, petiole, and apically on the metasoma; the medial part of the metasoma is a characteristic deep reddish to orangish-brown, and the wings are hyaline to slightly infumate. It is further recognized by the broad fenestra with a single, posteriorly positioned, oval sclerite (Fig. 16).

***Enicospilus kauaiensis* (Ashmead),  
new combination**

Fig. 17

*Pycnophion kauaiensis* Ashmead 1901: 344. Lectotype (designated by Townes et al. 1961: 295) female, Kauai, 4000 ft, VII.[18]96 (BMNH). Gupta 1987: 505. Yu and Horstmann 1997: 761.

**Remarks.**—This rare species is easily recognized by the combination of its small size (fore wing length about 8.0 mm); dark brown to black coloration (including face, clypeus and gena), weakly to distinctly infumate wings (particularly apically); long, upcurved ovipositor; evenly collicu-

late propodeum; and discosubmarginal cell without a fenestra or sclerite (Fig. 17).

***Enicospilus lineatus* (Cameron)**

Figs 18, 19, 37

*Ophion lineatus* Cameron 1883: 192. Lectotype (designated by Townes et al. 1961: 279 [Their usage of "type" is herein regarded as equivalent to a lectotype designation (ICZN 1999: Art. 74.5).]) female [metasoma absent], Lanai, (BMNH); transferred to *Henicospilus* by Morley 1912 and to *Enicospilus* by Perkins 1915. Blackburn and Cameron 1886: 179. Blackburn and Cameron 1987: 240. Ashmead 1901: 341. Dalla Torre 1901: 192. Szépligeti 1905: 31.

*Enicospilus mauicola* Ashmead 1901: 347. Lectotype (designated by Townes et al. 1961: 279) female, Molokai, Mts, 4500 ft (USNM); synonymized with *E. lineatus* (Cameron) by Cushman 1944. Perkins 1907a: 44. Perkins 1915: 526.

*Enicospilus henshawi* Ashmead 1901: 349. Lectotype (designated by Townes et al. 1961: 279 [Their usage of "type" is herein regarded as equivalent to a lectotype designation (ICZN 1999: Art. 74.5).]) female, Hawaii [Is.], Hilo, May (lost); synonymized with *E. lineatus* (Cameron) by Perkins 1915.

*Enicospilus dimidiatus* Perkins 1902: 143. Lectotype (designated by Townes et al. 1961: 279 [Their usage of "type" is herein regarded as equivalent to a lectotype designation (ICZN 1999: Art. 74.5).]) female, Oahu, Wailua [published as Ko'olau range], 1500 ft, R.C.L.P. [Perkins] (BPBM) [examined]; synonymized with *E. mauicola* Ashmead by Perkins 1915 and with *E. lineatus* by Cushman 1944. Perkins 1907a: 44. Perkins 1910: 679.

*Henicospilus mauicola* (Ashmead); Szépligeti 1905: 27.

*Henicospilus dimidiatus* (Perkins); Szépligeti 1905: 27. Morley 1912: 52.

*Henicospilus henshawi* (Ashmead); Szépligeti 1905: 27.

*Enicospilus capnodes* Perkins 1910: 679. Lectotype (designated by Townes et al. 1961: 279 [Their usage of "type" is herein regarded as equivalent to a lectotype designation (ICZN 1999: Art. 74.5).]) male, Hawaii [Is.], Kona, 1000 ft, (BPBM) [examined]; synonymized with *E. mauicola* Ashmead by Perkins 1915 and with *E. lineatus* by Cushman 1944.

*Henicospilus lineatus* (Cameron); Morley 1912: 47, 52. Uchida 1928: 219. Chu 1935: 14. Uchida 1937: 11. [All misidentifications of *Enicospilus lineolatus* (Roman) (according to Gauld and Mitchell 1981, and Gupta 1987) except second reference by Morley (page 52).]

*Enicospilus funereus* Perkins 1915: 525. Lectotype (here designated) female, w. [West] Maui, 1500 ft, III.02, R.C.L.P. [Perkins] (BPBM) [examined] [Townes et al. 1961: 279 erroneously described syntypes from other islands.]; synonymized with *E. lineatus* (Cameron) by Townes et al. 1961. Swezey and Williams 1932: 182. Cushman 1944: 51.

*Enicospilus lineatus* (Cameron); Perkins 1915: 526. Cushman 1944: 50. Iwata 1950 [misidentification, likely of *Enicospilus lineolatus* (Roman)]. Townes et al. 1961: 279. Lee and Kim: 1980: 11 [misidentification, likely of *Enicospilus lineolatus* (Roman)]. Gauld and Mitchell 1981: 8. Gupta 1987: 548. Yu and Horstmann 1997: 743.

*Enicospilus ashmeadi* Perkins 1915: 527. Lectotype (designated by Townes et al. 1961: 279) female, Hawaii [Is.], Kilauea, VII.03, (BPBM) [examined]; synonymized with *E. lineatus* (Cameron) by Cushman 1944. Anonymous 1925: 11.

**Remarks.**—This species displays an impressive amount of variation in features including size (fore wing length 8.5–16.4 mm), color (monochrome or mixed, ranging from dark brown or almost black to reddish-brown or orange, with frequent exception of yellowish areas of the face and gena; wings vary from slightly to strongly infumate), and the form of the alar sclerite (Figs 18, 19). This was pointed out by Cushman (1944) who synonymized a number of names under *E. lineatus*. Additional specimen material and a focused study of the variation and distribution of forms could potentially reveal cryptic species and/or forms representing early phases of divergence.

***Enicospilus longicornis* Ashmead**

Figs 20, 36

*Enicospilus longicornis* Ashmead 1901: 350. Lectotype (designated by Townes et al. 1961: 280 [Their usage of "type" is herein regarded as

equivalent to a lectotype designation (ICZN 1999: Art. 74.5).]) male [labeled as female], Hawaii [Is.], Kilauea (BMNH). Perkins 1915: 524. Swezey and Williams 1932: 182. Townes et al. 1961: 280. Gupta 1987: 551. Yu and Horstmann 1997: 743.

*Enicospilus longicornis* (Ashmead); Szépligeti 1905: 27.

*Enicospilus tyrannus* Perkins 1910: 678. Lectotype (designated by Townes et al. 1961: 292 [Their usage of "type" is herein regarded as equivalent to a lectotype designation (ICZN 1999: Art. 74.5).]) female, Molokai, 4000 ft, II.02 (BPBM) [examined]; **new synonymy**. Perkins 1915: 524. Anonymous 1925: 11. Swezey and Williams 1932: 182. Cushman 1944: 53. Townes et al. 1961: 293. Yu and Horstmann 1997: 752.

*Enicospilus* (*Enicospilus*) *longicornis* Ashmead; Cushman 1944: 52.

**Remarks.**—This medium-sized to large species (forewing length 10.1–19.5 mm) is easily recognized by the distinctly down-curved ovipositor, heavily setose, diagonal groove of the mandible (Fig. 36), and at least two prominent alar sclerites (Fig. 20). The gena (widely), face below the toruli, and often the clypeus are largely yellow with the possible exception of the medial area; the mesosoma varies from orange to red-dish-brown throughout (typically in the smaller individuals) to a patchwork of brownish-yellow and dark brown areas; the metasoma varies from orange or reddish-brown to dark brown, either similar throughout or with the petiole noticeably darker; and the wings vary from slightly to distinctly infumate, often with a yellowish tint. As suspected by Cushman (1944), *E. tyrannus* represents the larger individuals among a continuum of variation in size and color.

### *Enicospilus melanochromus* Perkins

Fig. 21

*Enicospilus melanochromus* Perkins 1915: 523. Lectotype (designated by Townes et al. 1961: 281 [Their usage of "type" is herein regarded as equivalent to a lectotype designation

(ICZN 1999: Art. 74.5).]) female, Maui, Haleakala, 2500 ft, III.02, R.C.L.P [Perkins] (BPBM) [examined]. Townes et al. 1961: 281. Gupta 1987: 554. Yu and Horstmann 1997: 744.

*Enicospilus* (*Enicospilus*) *melanochromus* Perkins; Cushman 1944: 47.

**Remarks.**—This medium-sized (fore wing length 9.1–10.5 mm) and rarely collected species is similar to *E. blackburni* but can be distinguished from the latter by its usual dark brown coloration (with possible exception of a yellowish face, clypeus and gena; one individual examined is orangish-brown throughout as in *E. blackburni*), moderately infumate wings, fore wing with a basally expanded fenestra (Fig. 21) and 1m-cu without an angle medially (though often thickened), and the apically swollen aedeagus.

### *Enicospilus minimus*, new species

Fig. 7A–E

**Diagnosis.**—Owing to its unusual habitus, the difficulty in diagnosing this species for the uninitiated will be in recognizing it as an ophionine, and not one of the many small, introduced ichneumonoids among the Hawaiian fauna. Its small size, yellow and brown coloration, reduced ocelli, and vestigial fenestra allow for its identification to species.

**Description.**—Length of fore wing 3.7–4.3 mm in female. **Head:** Mandible moderately stout, more or less parallel-sided medially, weakly twisted; basal, ventral margin strongly concave; outer surface without strong basal concavity, sparsely setose with hairs scattered or aggregated medially but not along a distinct diagonal groove; upper tooth long, 1.7–1.8× as long as lower tooth, about as wide as lower tooth at base. Labrum concealed in examined specimens. Malar space 0.5× as long as basal mandibular width. Clypeus in profile weakly to strongly convex, proximal margin distinct from lower face; in frontal view 2.3–2.4× as broad as long,

colliculate, apical margin broadly flat, sharp, impressed medially. Lower face as broad as long, evenly colliculate. Compound eye reduced, head width in frontal view  $1.3\text{--}1.4\times$  length (Fig. 7A). Gena with setae short, inconspicuous and declined forward; in dorsal view very broadly rounded behind compound eye (Fig. 7B),  $GO = 1.1\text{--}1.4$ . Ocelli small, posterior ocellus removed from compound eye by  $0.8\text{--}0.9\times$  its diameter,  $FI = 0.2\text{--}0.3$ . Occipital carina dorsally rounded, ventrally ending well short of hypostomal carina. Flagellum in female  $1.5\text{--}1.6\times$  length of fore wing, with 30–33 segments, mid segment  $2.3\text{--}2.5\times$  as long as broad. **Mesosoma:** Mesoscutum strongly rounded anteriorly in profile, anterior angle about  $90^\circ$ ; notauli not impressed (though marked by darker color). Scutellum compact, in dorsal view  $1.1\text{--}1.2\times$  as long as anterior width; upper surface strongly convex, evenly colliculate, lateral carinae present only anteriorly, extending about  $1/10$  scutellar length; posterior declivity smooth or weakly striate, angled by about  $45^\circ$  in profile. Mesopleuron evenly colliculate throughout, evenly rounded with little variation in relief; scrobe small, distinct or indistinct, not set in shallow groove, speculum not apparent; mesopleural sulcus with weak transverse marks; epicnemial carina strong, complete medioventrally. Mesosternum without lateral longitudinal depression; with posterior transverse carina present medioventrally. Lower metapleuron moderately convex, evenly colliculate. Propodeum in profile weakly to moderately rounded anteriorly, flat medially and posteriorly; sparsely setose with setae low, inconspicuous, posteriorly declined; spiracle small, oval; anterior furrow shallow, rugostriate,  $0.1\text{--}0.2\times$  total propodeal length; anterior transverse carina absent or present as a vestigial medial remnant, posterior transverse carina absent; spiracular area evenly colliculate,  $0.2\text{--}0.3\times$  total propodeal length; posterior area coarsely or evenly colliculate, becoming rugulose or

rugulostriate posteriorly and posterolaterally. Separation between propodeum and lower metapleuron indicated by a complete furrow, not accompanied by a carina. Fore wing (Fig. 7C) with pterostigma short, wide, abruptly narrowed; discosubmarginal cell without sclerites, fenestra fairly small, round (ill-defined in one specimen examined), apical margin extending beyond midpoint of  $Rs+2r$ , posterior margin extending to about midway between  $Rs+2r$  and  $1m\text{--}cu$  or to nearer  $1m\text{--}cu$ ;  $Rs+2r$  straight or slightly arched, thickened in basal half  $1/2$  to  $3/4$ ;  $Rs+M$  slightly arched in basal half;  $1m\text{--}cu$  evenly arched;  $3r\text{--}m$  absent or reduced to such extent that  $AI$  is about  $3.2$ ;  $CI = 0.4\text{--}0.6$ ;  $ICI = 0\text{--}0.4$ ;  $SDI = 0.8\text{--}0.9$ ;  $cu\text{--}a$  anterior of  $Rs+M$  by  $0.5\text{--}0.7$  length of  $cu\text{--}a$ ; 1st subdiscal cell with a setae sparse and even in ventral half, lacking in anterior half. Hind wing (Fig. 7E) with 1<sup>st</sup> abscissa of  $Rs$  straight, 2<sup>nd</sup> abscissa entirely nebulous, nearly straight, continuing to wing margin; 2<sup>nd</sup> abscissa of  $Cu1$  emerging much nearer  $1A$  than  $M$ ,  $CI = 0.1\text{--}0.2$ ;  $1A$  absent distal of  $cu\text{--}a$ . Fore leg tibia  $7.8\text{--}8.2\times$  as long as wide, without subapical spines on outer surface. Mid leg with coxa evenly colliculate; inner tibial spur about  $1.3\times$  as long as outer spur. Hind leg with coxa in lateral view  $1.7\times$  as long as deep, evenly colliculate; trochantellus dorsally about  $0.4\times$  as long as broad; 4<sup>th</sup> tarsomere in female  $2.2\text{--}2.5\times$  as long as broad in dorsal view; 5<sup>th</sup> tarsomere of female in dorsal view evenly broadened distally,  $4.5\text{--}6.0\times$  as long as broad, in lateral view nearly straight; pretarsal claw of female approximately as figured (Fig. 7D). **Metasoma:** Fairly compact and apically deep in female;  $T2$  in female  $2.4\text{--}3.3\times$  as long as lateral height,  $2.5\text{--}3.0\times$  as long as dorsal width; thyridium tear-shaped to elliptical, positioned posterior of anterior margin of  $T2$  by  $0.2\times$  length of  $T2$ . Ovipositor short and straight, about  $0.8\times$  length of  $T2$ .

**Color:** Head yellowish-brown, darker near ocelli, on frons, and gena; mesosoma trunk and legs brown and yellow; wings hyaline.



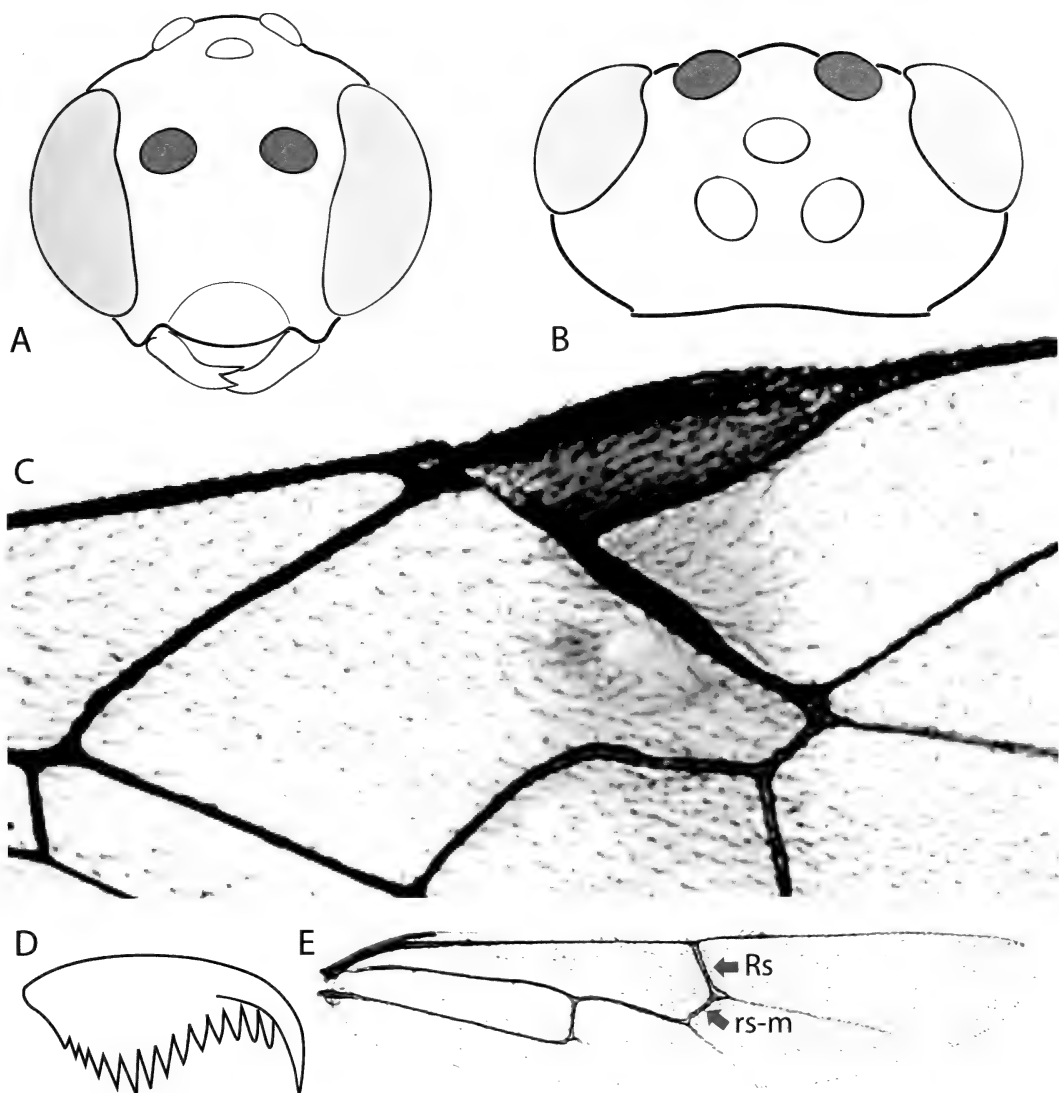


Fig. 7. *Enicospilus minimus*: A, frontal aspect of head; B, dorsal aspect of head; C, discusubmarginal cell of fore wing; D, female hind outer claw; E, hind wing.

**Remarks.**—The minute size of *E. minimus* is unique among *Enicospilus* and probably Ophioninae in general. Its reduction has resulted in the extreme contraction of vein 3r-m of the fore wing, the presence of which is a synapomorphy for the subfamily (Gauld 1985). It is, however, recognizable as an *Enicospilus* owing to the slight twist of the mandible, vestigial fenestra, and the extension of the posterolateral area of the pronotum over the pronotal spirac-

ular sclerite. It seems to be allied to the other Hawaiian *Enicospilus* species and particularly resembles *E. petilus* in head shape and color pattern. Furthermore, it possesses the general apomorphic features for Hawaiian *Enicospilus* (colliculate punctation and loss of fore-tibial spines).

**Material examined.**—**Holotype:** female, Hawaii, **Hawaii Is.:** Near Wauhaula Heiau, 7 December 2006, (W. C. Gagné) (BPBM). **Para-**

**type:** female, Oahu, Waimano Trail, 1900 ft elevation, 1 February 1970 (W. C. Gagné) (BPBM).

**Etymology.**—The species epithet is Latin for “small”, in reference to the minute size of this species as compared to all other *Enicospilus* species.

*Enicospilus molokaiensis* (Ashmead),  
new combination  
Fig. 22

*Pycnophion molokaiensis* Ashmead 1900: 87. Lectotype (herein designated) female, Molokai, Mts, 4500 ft, 7[?] IX 1893, Perkins (AEIC) [examined]. Ashmead 1901: 344. Dalla Torre 1901: 185. Szépligeti 1905: 71. Anonymous 1925: 11. Cushman 1947: 461. Townes 1957: 117. Townes et al. 1961: 295. Townes 1971: 80. Gauld 1985: 168. Gupta 1987: 505. Yu and Horstmann 1997: 761.

**Remarks.**—This species can be easily recognized by the combination of its stout form; moderately large size (fore wing 9.8–11.8 mm); large compound eyes; long, upcurved ovipositor; weakly setose fore wing (at least proximally); discosubmarginal cell without a distinct fenestra or sclerites (Fig. 22); evenly colliculate propodeum; and weak or absent medial part of the posterior carina of the mesosternum. It is largely black with possible exceptions of the face, gena, and clypeus which usually contain yellow or whitish areas; the fore leg, mid leg, and anterolateral and ventral areas of the mesosoma are usually red to orange in part, and the wings are distinctly infumate.

This combination is not to be confused with its junior homonym *Enicospilus molokaiensis* Ashmead 1901 (= *E. blackburni* Bennett). Townes et al. (1961) and Gupta (1987) include a record from Hawaii Island as part of Ashmead's syntype set, but I believe this is not correct. Ashmead (1901) did not list such a record in his publication, and I have seen no evidence indicating that this species occurred there.

*Enicospilus niger* (Ashmead),  
reinstated combination  
Figs 23, 24

*Banchogastra nigra* Ashmead 1900: 87. Holotype (by monotypy) female, Hawaii [Is.], Kilauea, IX.[18]95 (BMNH); transferred to *Enicospilus* by Townes 1945, and Townes et al. 1961. Ashmead 1901: 343. Dalla Torre 1901: 185. Szépligeti 1905: 71. Anonymous 1913: 203. Anonymous 1925: 11. Cushman 1947: 460. Townes 1971: 79. Gauld 1985: 169. Gupta 1987: 505. Yu and Horstmann 1997: 730.

*Banchogastra nigri* [!] Ashmead; Perkins 1907b: 97.

*Enicospilus niger* (Ashmead); Townes 1945: 737. Townes 1957: 102. Townes et al. 1961: 283.

**Remarks.**—This species is known from only a handful of specimens, and to my knowledge, it has not been collected since 1922. It can be recognized by the combination of its moderate size (fore wing length about 11.5 mm); highly stout form; compact and apically bulbous petiole that is further described in the key (Fig. 34); T2 wider than long in dorsal view; reduced compound eye; discosubmarginal cell of fore wing densely setose throughout without a fenestra or sclerite; coarsely rugose, areolate, or rugostriate propodeum with a strong anterior transverse carina; mid coxa without strong ridges dorsomedially; short, straight ovipositor; and coloration (head and mesosoma black, metasoma black to deep reddish-brown throughout, fore wing dark brown anteriorly, lighter in posterior, apical area).

*Enicospilus nigrolineatus* Ashmead  
Fig. 24

*Enicospilus nigrolineatus* Ashmead 1901: 348. Lectotype (designated by Townes et al. 1961: 284) male, Lanai, 2000 ft, 1.1894, Perkins (BMNH); Perkins 1915: 524. Townes et al. 1961: 284. Gupta 1987: 559. Yu and Horstmann 1997: 746.

*Henicospilus nigrolineatus* (Ashmead); Szépligeti 1905: 27.

*Enicospilus* (*Enicospilus*) *nigrolineatus* Ashmead; Cushman 1944: 52.

**Remarks.**—This large species (fore wing length 12.5–16.5 mm) can be easily recognized by its light brown to yellow coloration with the exception of a dark brown or black line laterally on the metasoma and the following black areas: scutum medially, mesosternum, and propodeum dorsomedially; wings are more or less hyaline. The second alar sclerite is linear and lies along the posterior, apical margin of the fore wing fenestra (Fig. 24). *Enicospilus variegatus*, which can be similar in this respect, is always more extensively covered in dark brown or black areas (see below).

***Enicospilus orbitalis* (Ashmead)**

Fig. 25

*Eremotylus orbitalis* Ashmead 1901: 345. Lectotype (designated by Townes et al. 1961: 285) female, Kauai, 2000–3000 ft, I.II.[18]97 (BMNH); transferred to *Eremotylodes* by Perkins 1915 [Perkins didn't state a type species for his *Eremotylodes* but he apparently intended it to be *E. orbitalis* Ashmead 1901 (see also discussion in Cushman 1947: 472)]. Szépligeti 1905: 36. Swezey and Bryan 1927: 412.

*Eremotylodes orbitalis* (Ashmead); Perkins 1915: 532. Anonymous 1925: 11. Swezey and Williams 1932: 182.

*Enicospilus* (*Eremotylodes*) *orbitalis* (Ashmead); Cushman 1944: 44.

*Enicospilus orbitalis* (Ashmead); Townes 1945: 737. Cushman 1947: 472. Townes et al. 1961: 285. Gupta 1987: 562. Yu and Horstmann 1997: 746.

**Remarks.**—This small to medium-sized species (fore wing length 6.5–11.5 mm) is relatively common in areas such as Kauai's Alakai swamp. It can be easily recognized by the combination of an extremely slender metasoma (dorsomedial length of exposed portion of T5 in female, T4 in male, greater than lateral depth) and the forewing discosubmarginal cell with a rather small, round fenestra lacking a sclerite (Fig. 25). Additionally, the ovipositor is short and slightly or distinctly upcurved; coloration is more or less evenly brown throughout,

with the possible exception of the face, clypeus, and gena, which are usually narrowly or broadly yellowish; and the wings are hyaline to slightly infumate.

***Enicospilus perkinsi* Cushman**

Fig. 26

*Enicospilus* (*Eremotylodes*) *perkinsi* Cushman 1944: 44. Holotype (by original designation) female, July 6, 1937, E. C. Zimmerman Oahu, at light (BPBM).

*Enicospilus perkinsi* Cushman; Townes et al. 1961: 286. Gupta 1987: 564. Yu and Horstmann 1997: 747.

**Remarks.**—This rarely collected, medium-sized species (fore wing length 9.0–11.0 mm) is easily recognized by the combination of an extremely slender metasoma (dorsomedial length of exposed portion of T5 in female, T4 in male, greater than lateral depth) and the distinctly orange head and metasoma which contrast with the darker metasoma (at least apically). Additionally, the ovipositor is upcurved; the fore wing discosubmarginal cell contains a round fenestra and a distinct, oval sclerite (Fig. 26); and the wings are slightly infumate, with a yellowish tint.

***Enicospilus petilus*, new species**

Fig. 8A–D

**Diagnosis.**—This species can be easily recognized by its greatly attenuated metasoma and very large proximal alar sclerite (Fig. 8D).

**Description.**—Length of fore wing 7.0–8.3 mm in female, 6.3–7.7 mm in male. **Head:** Mandible moderately stout, moderately twisted; basal ventral margin moderately to rather strongly concave; outer surface with a moderate basal concavity, sparsely to moderately setose along a weak diagonal groove; upper tooth 1.0–1.3× as long as lower tooth, about as wide or slightly narrower than lower tooth at base. Labrum 0.2–0.3× as long as broad, apical margin broadly rounded or flat medially.

Malar space  $0.5\text{--}0.6\times$  as long as basal mandibular width. Clypeus in profile nearly flat to weakly convex, proximal margin weakly to moderately distinct from lower face; in frontal view  $1.6\text{--}2.0\times$  as broad as long, lightly punctate and finely colliculate, apical margin broadly rounded or broadly flat, sharp, not impressed medially. Lower face  $0.9\text{--}1.2\times$  as broad as long. Compound eye reduced, head width in frontal view  $1.2\text{--}1.3\times$  length (Fig. 8A). Gena with setae inconspicuous, short, pale, and declined forward; in dorsal view broadly rounded behind compound eye (Fig. 8B),  $\text{GOI} = 1.5\text{--}2.3$ . Ocelli reduced, posterior ocellus separated from compound eye by  $0.4\text{--}0.6\times$  its diameter,  $\text{FI} = 0.3\text{--}0.4$ . Occipital carina dorsally flat or rounded, ventrally joining or ending short of hypostomal carina. Flagellum in female  $1.3\times$  length of fore wing, with 43–45 segments, mid segment  $2.3\text{--}2.5\times$  as long as broad; in male  $1.3\text{--}1.5\times$  length of fore wing, with 41–44 segments, mid segment  $2.3\text{--}2.4\times$  as long as broad. **Mesosoma:** Mesoscutum strongly rounded anteriorly in profile; notauli weak or not apparent. Scutellum short, rounded, in dorsal view  $1.1\text{--}1.3\times$  as long as anterior width; upper surface strongly convex, evenly and smoothly colliculate; lateral carinae more or less absent to weakly present through about  $1/2$  scutellar length; posterior declined by  $30^\circ\text{--}40^\circ$  in profile. Mesopleuron evenly colliculate throughout, rather flat and evenly rounded; scrobe small but clearly apparent, set in very shallow depression; speculum weakly apparent to absent; mesopleural sulcus with weak transverse ridges; epicnemial carina strong, medioventrally complete or narrowly absent. Mesosternum without lateral longitudinal depression behind epicnemial carina; with posterior transverse carina present medially. Lower metapleuron weakly to moderately convex, evenly colliculate to rugulose. Propodeum in profile weakly convex anteriorly and flat posteriorly to moderately convex throughout; exceeding-

ly sparsely setose (except one examined specimen moderate in this regard) with setae lying low and posteriorly declined; spiracle narrow; anterior furrow shallow, forming a broad concavity rather than a sharp groove, coarsely rugostriate, anterior area  $0.1\text{--}0.2\times$  total propodeal length; anterior transverse carina present or absent, posterior transverse carina absent or present; spiracular area finely colliculate, about  $0.3\times$  total propodeal length; posterior area anteriorly rugulose becoming rugostriate posteriorly. Separation between propodeum and lower metapleuron indicated by a weak furrow and weak, irregular carina. Fore wing (Fig. 8D) with pterostigma short and triangular, distal end narrowed abruptly; discosubmarginal cell with 2 sclerites, the basal one very large, semicircular or roughly triangular, the distal one linear, partially outlining distal ventral margin of fenestra; fenestra semicircular, extending apically to at least midpoint of  $\text{Rs}+2\text{r}$ , posterior margin extending to about  $2/3$  the distance between  $\text{Rs}+2\text{r}$  and  $1\text{m-cu}$ ;  $\text{Rs}+2\text{r}$  thickened medially and sinuous;  $\text{Rs}+\text{M}$  nearly straight or slightly arched in basal half;  $1\text{m-cu}$  evenly arched;  $\text{AI} = 1.5\text{--}2.1$ ;  $\text{CI} = 0.3\text{--}0.4$ ;  $\text{ICI} = 0.2\text{--}0.3$ ;  $\text{SDI} = 0.9\text{--}1.3$ ;  $\text{cu-a}$  positioned directly opposite base of  $\text{Rs}+\text{M}$ ; 1st subdiscal cell sparsely setose throughout or only in posterior part. Hind wing with 4–6 hamuli in distal set; 1<sup>st</sup> abscissa of  $\text{Rs}$  nearly straight or slightly concave basally, 2<sup>nd</sup> abscissa straight; 2<sup>nd</sup> abscissa of  $\text{Cu}1$  emerging much nearer  $1\text{A}$  than  $\text{M}$ ,  $\text{CI} = 0.2$ . Fore leg tibia  $7.7\text{--}8.7\times$  as long as wide, without an array of subapical spines on outer surface. Mid leg with coxa evenly colliculate; with inner tibial spur  $1.3\text{--}1.5\times$  as long as outer spur. Hind leg with coxa in lateral view  $1.6\text{--}1.7\times$  as long as deep; trochantellus dorsally  $0.3\text{--}0.5\times$  as long as broad; 4<sup>th</sup> tarsomere in female  $2.0\text{--}2.1\times$  as long as broad in dorsal view, about  $2.2\times$  in male; 5<sup>th</sup> tarsomere of female in dorsal view evenly broadened distally,  $2.8\text{--}3.1\times$  as long as broad, in lateral view weakly curved; 5<sup>th</sup>

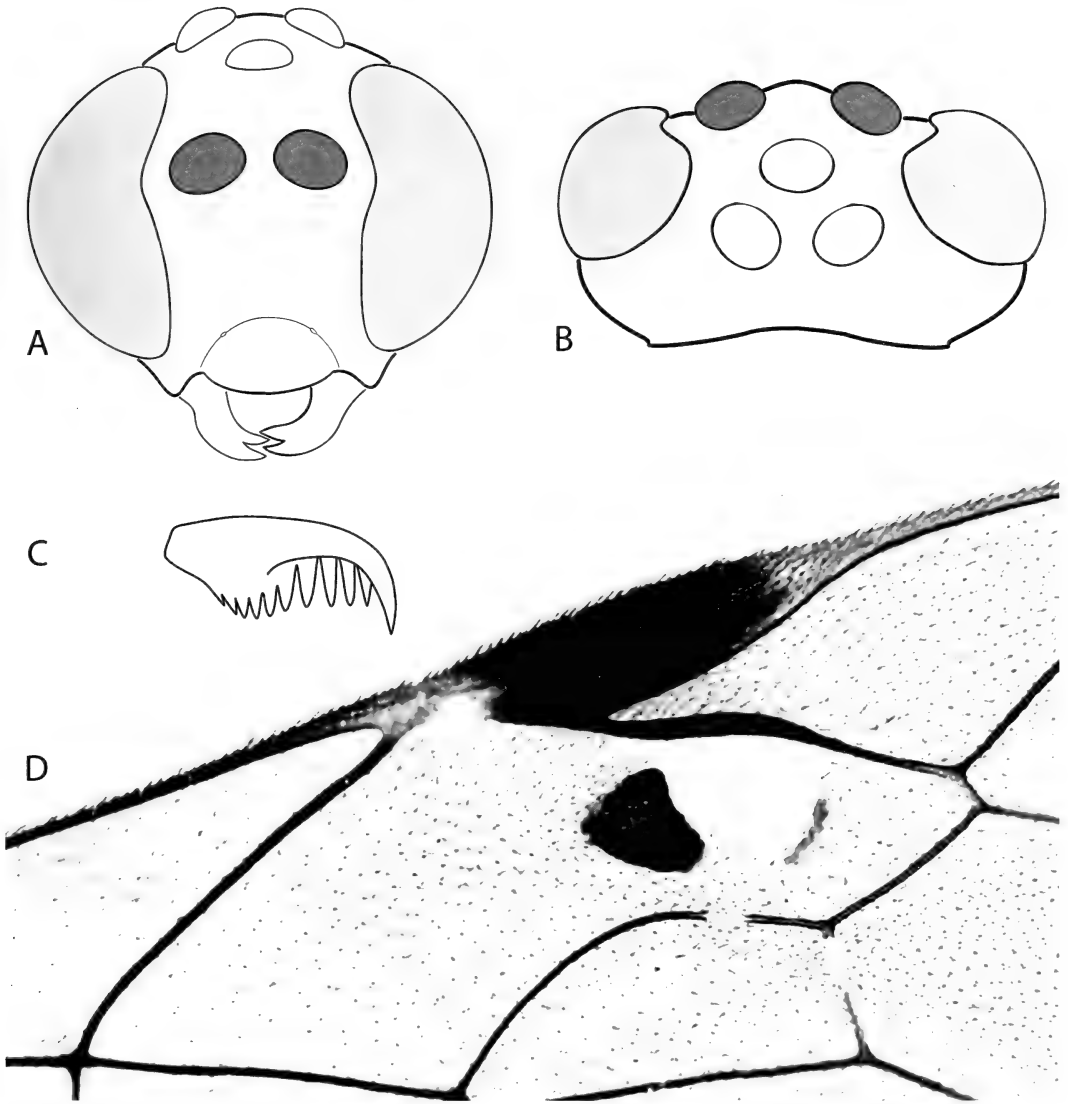


Fig. 8. *Enicospilus petilus*: A, frontal aspect of head; B, dorsal aspect of head; C, female hind outer claw; D, discosubmarginal cell of fore wing.

tarsomere of male in dorsal view somewhat abruptly widened apically, about  $3.5\times$  as long as broad, in lateral view weakly curved; pretarsal claw approximately as in Fig. 8C, apparently with little or no sexual dimorphism. **Metasoma:** Very elongate (especially in female), narrowed and laterally flattened apically in female; T2 in female  $4.3\text{--}5.3\times$  as long as lateral height,  $3.0\text{--}3.5\times$  as long as dorsal width; T2 in male about  $4.5\times$  as long as lateral height,  $2.4\text{--}4.9\times$  as long as dorsal width;

thyridium tear-shaped, positioned posterior of anterior margin of T2 by  $0.3\text{--}0.4\times$  length of T2. Ovipositor short and straight or slightly upcurved.

**Color:** Generally yellow and brown; head yellowish-brown, darker on dorsal gena and antenna; mesosoma brown with yellow patches on mesoscutum, medially on scutellum, and variously on mesopleuron and propodeum; wings hyaline; legs yellow to yellowish-brown with apical tarsomeres, hind coxa and femur (at least

in part) darker; metasoma with basal half or more of petiole pale yellow or yellowish-brown, otherwise brown except for various ill-defined lighter intersegmental areas which are lighter.

*Material examined*.—**Holotype**: female, Hawaii, **Maui**: Haleakala National Park, upper Kipahulu Valley, "Charlie Camp"; 1450 m elevation, 28 February–4 March 1984, UV light trap in forest (W. C. Gagné, S. Gon III) (BPBM). **Paratypes** (4): 1 female, **Hawaii**: Kilauea, "29 mi," August 1912 (W. M. Giffard) (AEIC); 1 female, **Molokai**: Pepeopae, 4000 ft elevation, 30 July 1959 (D. E. Hardy) (BPBM); 1 male, **Molokai**: West end of Hanalilolilo Trail, 1070 m, 7 January 1981, M. V. light, (W. C. Gagné) (BPBM); 1 male, **Hawaii**: Manuka Forest Reserve, South Kona, Kopua T. [Trail?], 3600 ft elevation, 22 June 1977, night, (R. S. Villegas and S. M. Gon III) (BPBM).

*Etymology*.—The species epithet, a Latin adjective for "slender," is in reference to the extremely elongate metasoma of the female.

### *Enicospilus pseudonymus* Perkins

Fig. 27

*Enicospilus pseudonymus* Perkins 1915: 529. Lectotype (designated by Townes et al. 1961: 286 [Their usage of "type" is herein regarded as equivalent to a lectotype designation (ICZN 1999: Art. 74.5).]) male, Maui, Haleakala, 4000 ft (BPBM) [examined]. Anonymous 1925: 10. Cushman 1944: 53. Townes et al. 1961: 286. Gupta 1987: 568. Yu and Horstmann 1997: 748.

*Remarks*.—This rarely collected, fairly large species (fore wing length 12.0–13.2 mm) can be recognized by the unique lateral, longitudinal depressions of the posterior mesonotum and scutellum. Additionally, the upper mandibular tooth is shorter than the lower tooth; the fore wing discosubmarginal cell lacks a sclerite and contains a fenestra which is at most a rather narrow, poorly defined region of reduced pubescence (Fig. 27); and the posterior transverse carina of mesosternum is absent or weak medially

(often weak medially and absent submedially). It is more or less orangish-brown with exception of the face, clypeus, and gena, which are largely yellow, as well as parts of the mesonotum, mesopleuron, propodeum, and petiole, which are often slightly or distinctly darker; the wings are hyaline.

### *Enicospilus swezeyi*, new name

Fig. 1

*Pycnophion fuscipennis* Perkins 1910: 680. Lectotype (designated by Townes et al. 1961: 295 [Their usage of "type" is herein regarded as equivalent to a lectotype designation (ICZN 1999: Art. 74.5).]) female, Kauai, 3000 ft, winter 1901 (BPBM) [examined]; preoccupied in *Enicospilus* by *E. fuscipennis* (Szépligeti 1906). Anonymous 1925: 11. Swezey 1931: 502. Townes et al. 1961: 295. Gupta 1987: 505. Yu and Horstmann 1997: 761.

*Pycnophion fumipennis* [!] Perkins; Cushman 1947: 462.

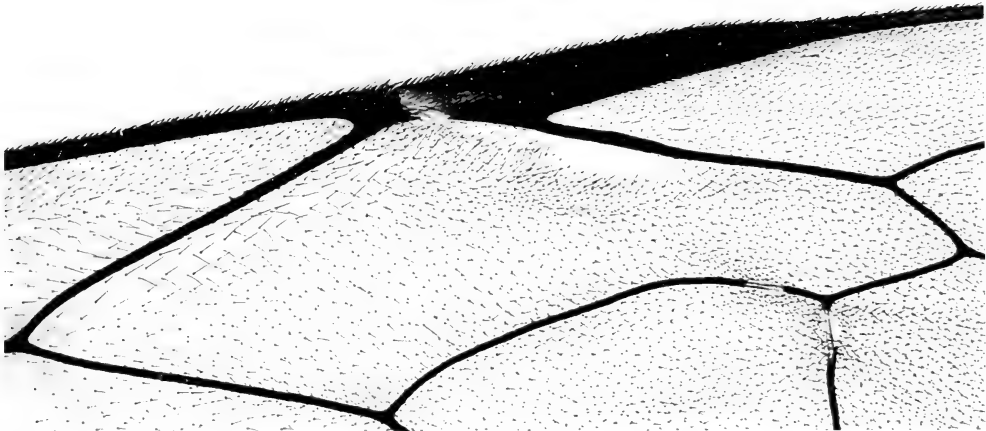
*Remarks*.—This distinctive, small to medium-sized species (fore wing length 8.2–10.7 mm) can be recognized by its highly contrasting red and black coloration (Fig. 1); a long, straight ovipositor; propodeum posteriorly rugose, without an anterior transverse carina, with posteriorly projecting setae dorsomedially; lack of both a sclerite and a clearly defined fenestra in the fore wing discosubmarginal cell; distinctly infumate wings; and a weak or absent posterior transverse carina of the mesosternum.

*Etymology*.—The new name is dedicated to the prolific Hawaiian entomologist, Otto Swezey, whose efforts in the rearing of Hawaiian insects over many years (Swezey 1954) resulted in many discoveries including the host for this species, as elaborated on above.

### *Enicospilus variegatus* Ashmead

Fig. 28

*Enicospilus variegatus* Ashmead 1901: 348. Lectotype (designated by Townes et al. 1961: 293) male, Hawaii [Is.], Ola'a, II.1896 (BMNH).



9. *Enicospilus bellator*



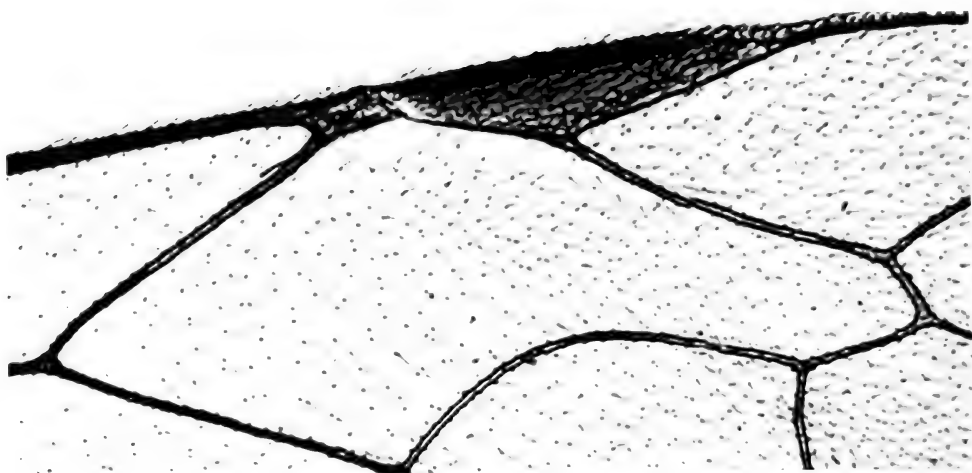
10. *Enicospilus blackburni*



11. *Enicospilus castaneus*

Figs 9–11. Fore wing discal cells.





12. *Enicospilus debilis*

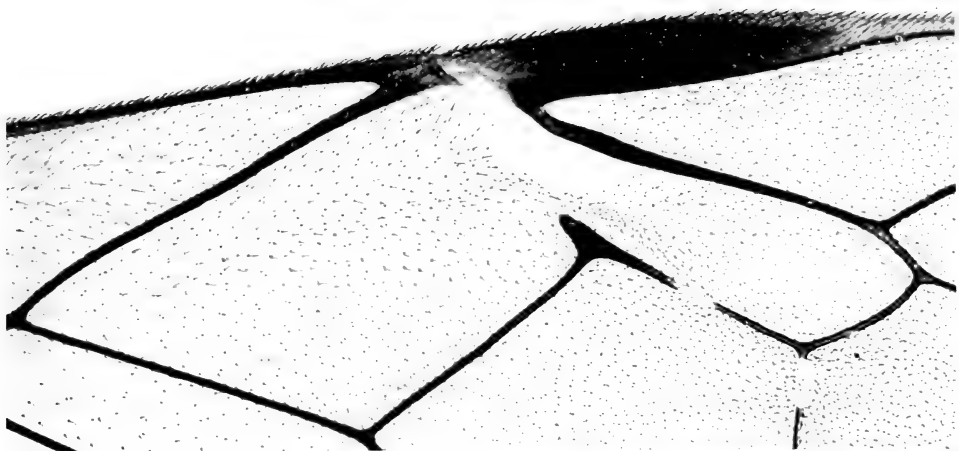


13. *Enicospilus dispilus*

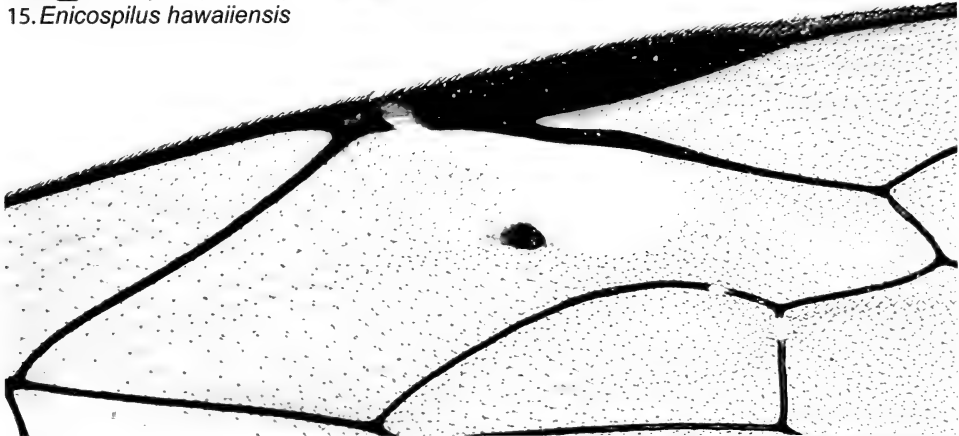


14. *Enicospilus fullawayi*

Figs 12–14. Fore wing discosubmarginal cells.



15. *Enicospilus hawaiiensis*



16. *Enicospilus kaalae*

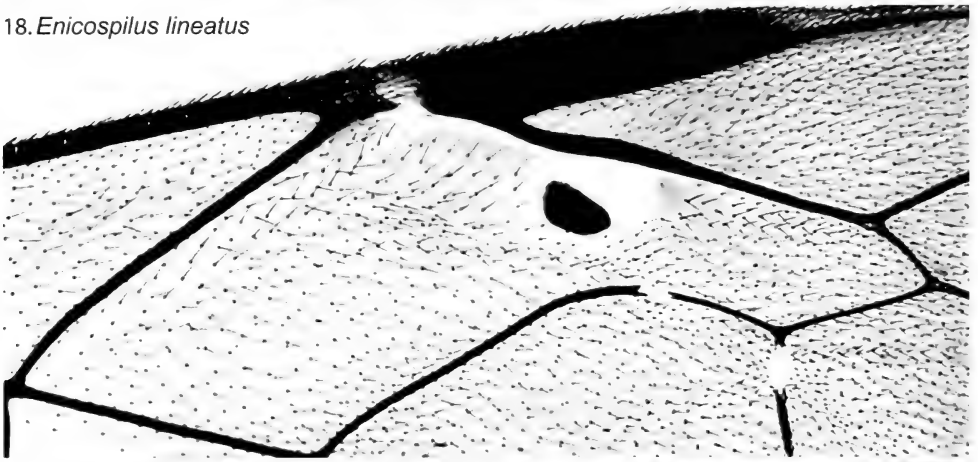


17. *Enicospilus kauaiensis*

Figs 15–17. Fore wing discal cells.



18. *Enicospilus lineatus*

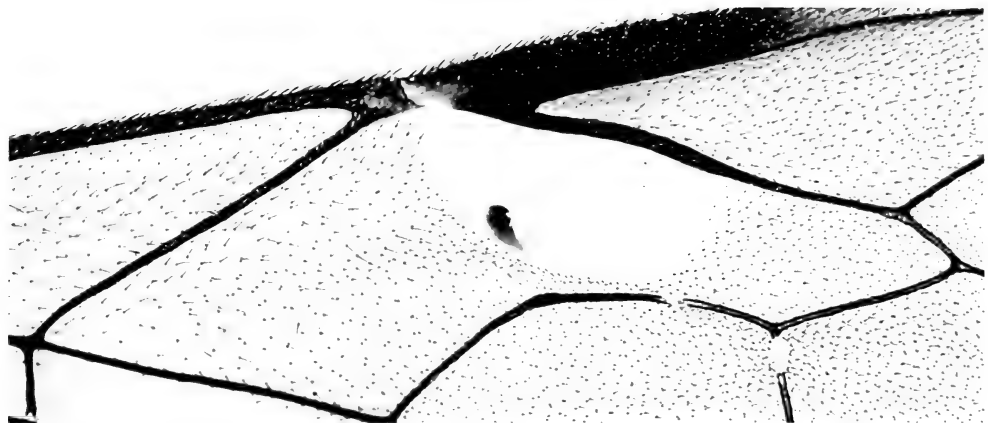


19. *Enicospilus lineatus*

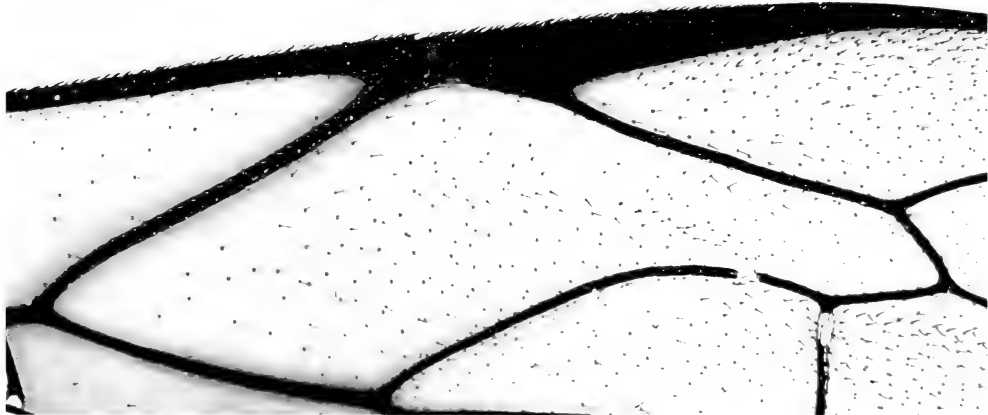


20. *Enicospilus longicornis*

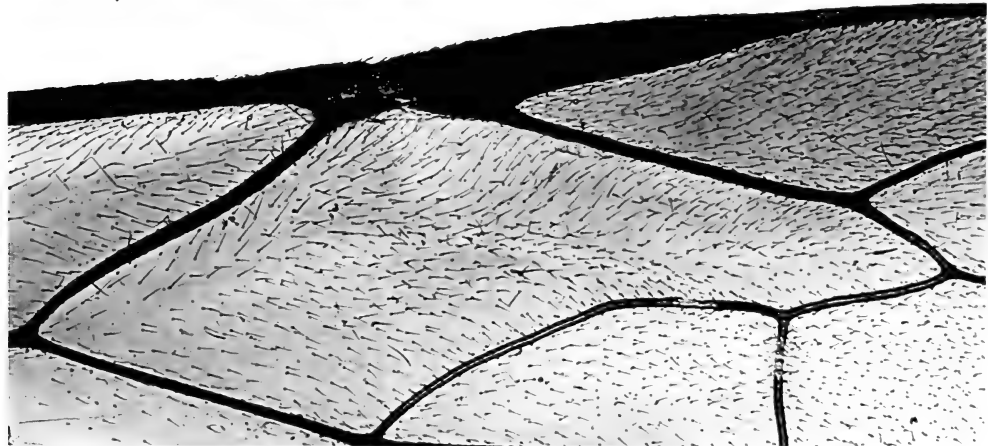
Figs 18–20. Fore wing discal cells.



21. *Enicospilus melanochromus*



22. *Enicospilus molokaiensis*

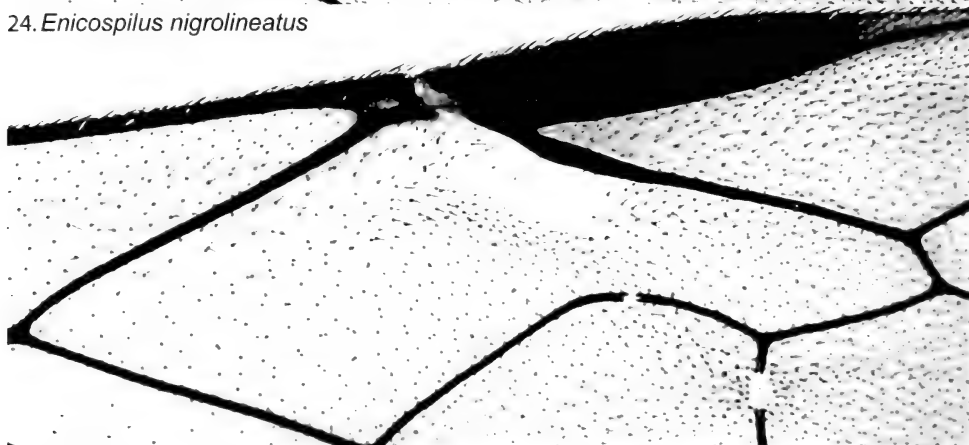


23. *Enicospilus niger*

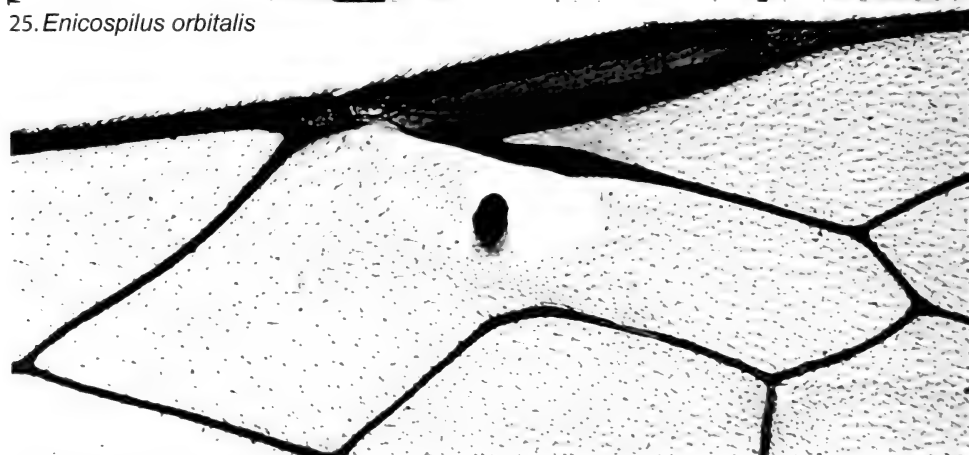
Figs 21–23. Fore wing discal cells.



24. *Enicospilus nigrolineatus*



25. *Enicospilus orbitalis*

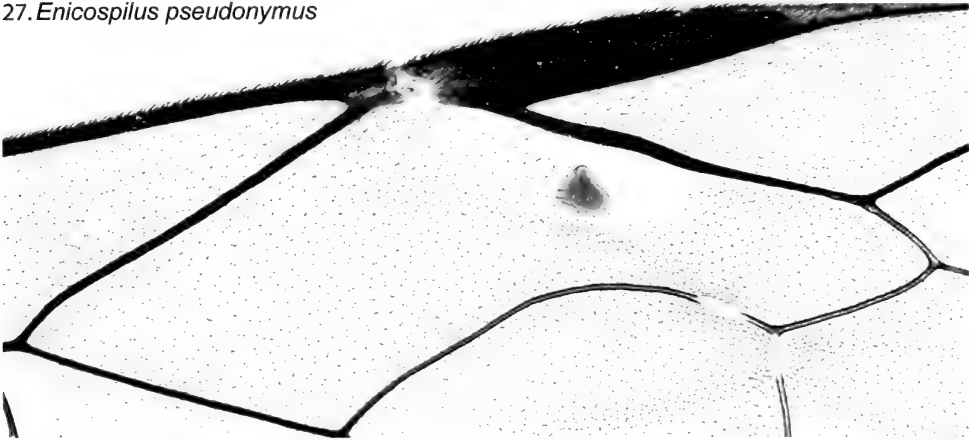


26. *Enicospilus perkinsi*

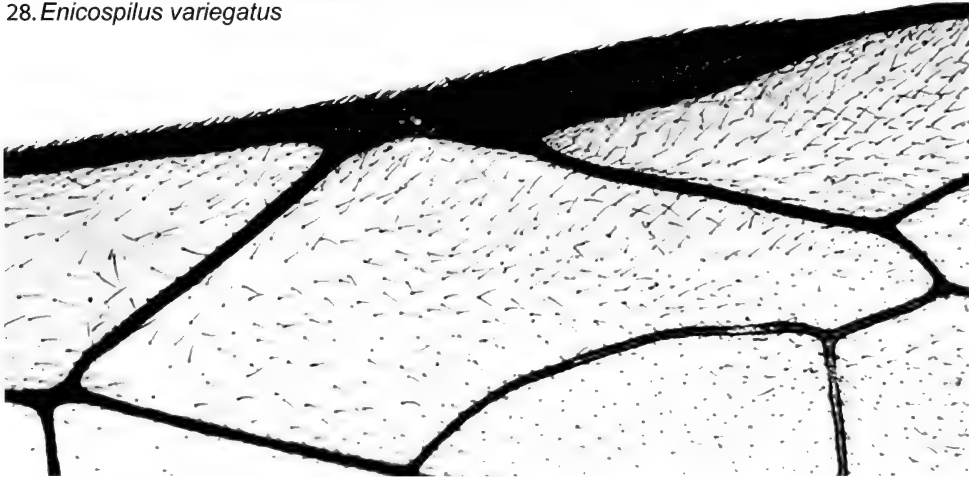
Figs 24–26. Fore wing discal cells.



27. *Enicospilus pseudonymus*

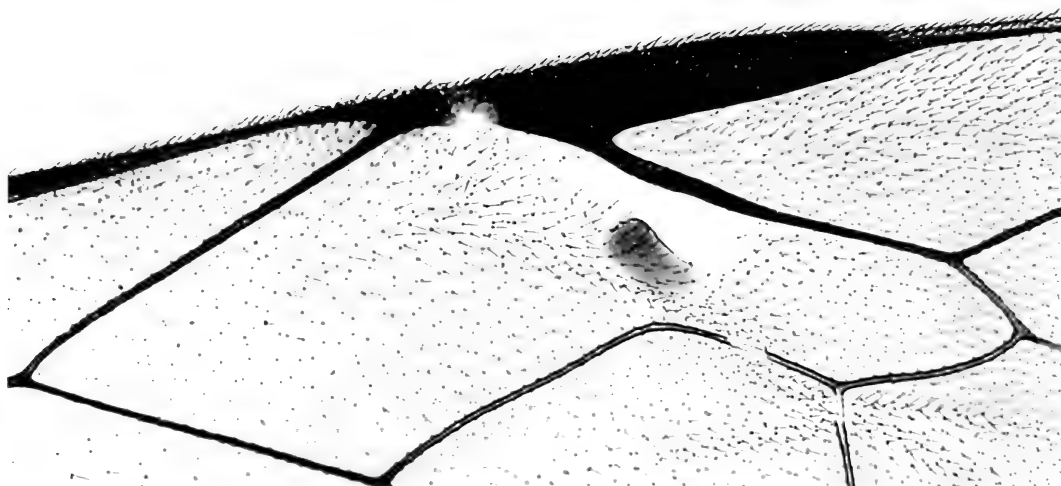


28. *Enicospilus variegatus*



29. *Enicospilus vitreipennis*

Figs 27–29. Fore wing discal cells.



30. *Enicospilus waimeae*

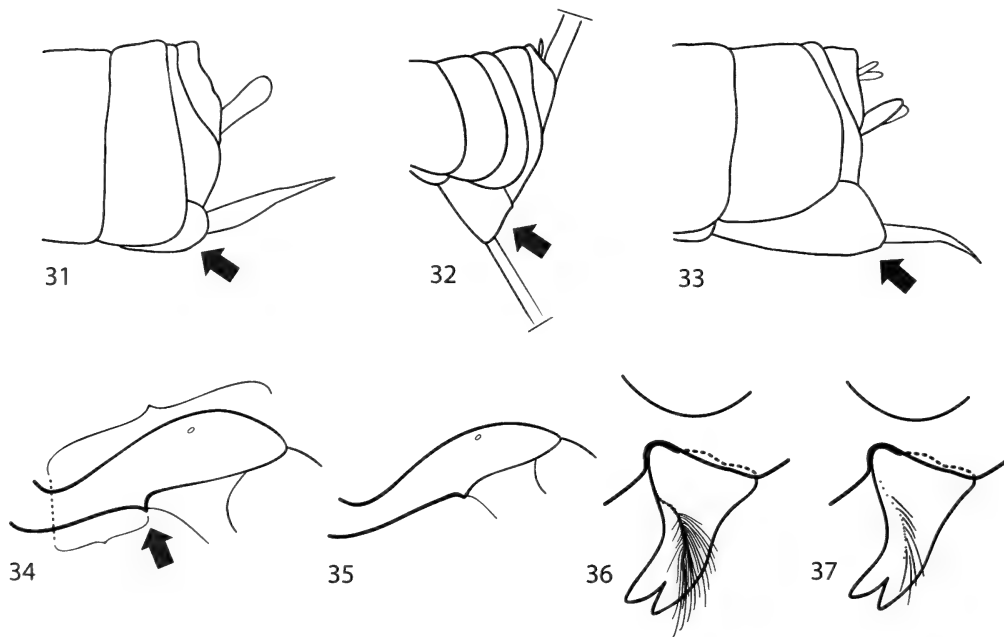


Fig. 30. Fore wing discal cell.

Figs 31–33. metasomal apices, arrows indicate S7.

Fig. 34. *Enicospilus niger* petiole in lateral view, arrow indicates ventral posterior margin, brackets indicate dorsal and ventral lengths.

Fig. 35. *Enicospilus vitreipennis* petiole in lateral view.

Fig. 36. *Enicospilus longicornis* mandible.

Fig. 37. *Enicospilus lineatus* mandible.

Perkins 1915: 525. Townes et al. 1961: 293.  
Gupta 1987: 583. Yu and Horstmann 1997:  
782

*Enicospilus* (*Enicospilus*) *variegatus* Ashmead;  
Cushman 1944: 51.

*Enicospilus variegatus* (Ashmead); Szépligeti  
1965: 7.

**Remarks.**—This large species (fore wing  
length 14.5–16.0 mm) can be recognized by



its highly contrasting color pattern. It is largely dark brown to black except for the following yellow or yellowish-brown areas: head, pronotum (in total or in part), mesonotum and scutellum in part, upper mesopleuron, metapleuron, anterodorsal part of propodeum, and legs (except for the femora apically, and with the possible exception of the apical tarsomeres). Additionally, the fore wing discosubmarginal cell contains a large, triangular, proximal sclerite and often a second, vestigial sclerite at the apical, posterior fenestral margin (Fig. 28); the wings are more or less hyaline.

*Enicospilus vitreipennis* (Perkins),  
reinstated combination  
Figs 29, 35

*Banchogastra vitreipennis* Perkins 1910: 680. Lectotype (designated by Townes et al. 1961: 293 [Their usage of "type" is herein regarded as equivalent to a lectotype designation (ICZN 1999: Art. 74.5).]) female, Maui, Haleakala, 5000 ft (BPBM) [examined]; transferred to *Enicospilus* by Townes et al. 1961. Gupta 1987: 506. Yu and Horstmann 1997: 730.

*Enicospilus vitreipennis* (Perkins); Townes et al. 1961: 293.

**Remarks.**—This small species (fore wing length 7.5–9.5 mm) can be recognized by the combination of its coloration (darkest brown to black throughout with the possible exception of the wings which vary from nearly hyaline to dark brown); short ovipositor; highly reduced compound eye; discosubmarginal cell usually without a trace of a fenestra and densely setose throughout; propodeum coarsely rugose, areolate, or rugostriate with a strong anterior transverse carina; mid coxa without strong dorsomedial ridges; posterior transverse carina of the mesosternum absent; T2 usually longer than wide in dorsal view; and, with respect to *E. niger*, a less compact, flatter petiole that is further described in the key (Fig. 35).

*Enicospilus waimeae* Ashmead  
Fig. 30

*Enicospilus waimeae* Ashmead 1901: 348. Lectotype (designated by Townes et al. 1961: 293) female, Kauai, Mts Waimea, 4000 ft, VI.1894, Perkins (BMNH); Perkins 1915: 525. Townes et al. 1961: 293. Gupta 1987: 586.

*Henicospilus waimae* [!] (Ashmead); Szépligeti 1905: 27.

*Enicospilus* (*Enicospilus*) *waimeae* Ashmead; Cushman 1944: 51.

**Remarks.**—This rarely collected, moderately large species (fore wing length 11.0–13.4 mm) is principally recognized by its single, extremely large sclerite of the fore wing discosubmarginal cell (Fig. 30). Additionally, it is generally slenderer than *E. lineatus* (to which it otherwise most closely resembles); is more or less brown throughout (becoming lighter brown on the face laterally, gena, tibiae, tarsi, and metasoma apically); has a short, straight ovipositor; and has slightly infumate wings.

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## The Description of Euceroptrinae, a New Subfamily of Figitidae (Hymenoptera), including a Revision of *Euceroptres* Ashmead, 1896 and the Description of a New Species

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**Abstract.**—The figitid genus *Euceroptres* Ashmead has recently been determined to render the Thrasorinae, a subfamily where the genus is currently classified, paraphyletic. To maintain the monophyly of Thrasorinae, *Euceroptres* is here redescribed and placed in its own subfamily, Euceroptrinae. All known species are redescribed and a new species is described; a lectotype is designated for *E. primus* Ashmead, 1896. The phylogenetics of Euceroptrinae, Parnipinae, Plectocynipinae and Thrasorinae are discussed, and the hypothesis that ancestral lineages of figitids attacked gall-inducing Hymenoptera is supported. Agastoparasitism among these lineages appears to be plesiomorphic. Though branch support is relatively low for inferring the precise branching order of the gall-inducer parasite lineages, the classification of problematic species is much improved.

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Resolving the early branching events separating the phytophagous Cynipidae from the entomophagous Figitidae (Hymenoptera: Cynipoidea) continues to challenge hymenopterists. Although cynipoids resolve phylogenetically within the entomophagous parasitoid Hymenoptera (Ronquist et al. 1999, Dowton and Austin 2001), the majority of Cynipidae are obligate phytophages, inducing spectacular galls on host plants in 17 families of angiosperms (Weld 1952, Liljeblad and Ronquist 1998, Ronquist 1999). Figitids associated with the gall community are important for understanding the early evolution of these lineages; Ronquist (1995a, 1999) and Buffington et al. (2007) discussed two ancestral groups of cynipoids, i.e., Parnipinae and Thrasorinae, that represent lineages whose biology lie somewhere between entomophagy and phytophagy. Further, these

lineages also represent figitid agastoparasites (parasitoids whose primary hosts are themselves close relatives (Ronquist 1994)), a life-history strategy rare among Figitidae. Hence, understanding the taxonomy, biology, and phylogenetics of these groups will elucidate the evolutionary origins of the phytophagous cynipid lineage.

The Thrasorinae have been the subject of a few recent studies attempting to clarify our accumulated knowledge on this group. Ronquist (1994) grouped several cynipoid genera together in what he called the 'figitoid inquilines'; later, in Ronquist (1999), these genera (*Euceroptres* Ashmead, *Thrasorus* Weld, *Myrtopsen* Dettmer, *Pegacynips* Brèthes and *Plectocynips* Diaz) were placed within Thrasorinae, a group that previously only contained *Thrasorus* (Kovalev 1994). Ros-Farré and Pujade-Villar (2007) removed *Pegacynips* and *Plectocynips* from Thrasorinae and placed them into the newly described Plectocynipinae, and de-

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scribed a new thrasorine genus, *Scutimica* Ros-Farré. 'Buffington (submitted) revises the Australian Thrasorinae and describes a new genus of thrasorines associated with galls on *Eucalyptus* spp.'

Ronquist (1999) suggested the placement of *Euceroptres* within Thrasorinae as tentative at best, given that the taxon lacks a number of synapomorphies the remaining taxa possess. In both Ros-Farré & Pujade-Villar (2007) and Buffington (submitted), *Euceroptres* Ashmead was determined not to be a thrasorine, leading Buffington (submitted) to render the taxon *incertae sedis*. Buffington et al. (2007) found weak support for *Euceroptres* to be included within Thrasorinae. Further, *Euceroptres* rendered Thrasorinae paraphyletic if morphological data were excluded. Based on the total evidence phylogeny of Buffington et al. (2007), if Plectocynipinae is recognized, Thrasorinae is rendered paraphyletic unless *Euceroptres* is excluded.

## MATERIALS AND METHODS

**Rearing methods.**—Fully developed galls were collected by us from *Quercus agrifolia* NZe (Fagaceae) in Eaton Canyon State Park, Pasadena, CA. All leaves were removed and bare galls were placed together with tissue paper in plastic zipper bags to collect emerging wasps. Non-reared material for examination was borrowed from institutions listed below.

**Descriptions.**—Morphological terminology follows that of Ronquist and Nordlander (1989), Fontal-Cazalla et al. (2002) and Buffington et al. (2007); cuticular surface terminology follows that of Harris (1979). Specimens were examined using a Leica Wild M10 with fluorescent lighting. Images for figures were obtained using an EntoVision Imaging Suite, which included a firewire JVC KY-75 3CCD digital camera mounted to a Leica M16 zoom lens via a Leica z-step microscope stand. This system fed image data to a desktop computer where Cartograph 5.6.0 (Microvision Instruments, France) was used to capture a

fixed number of focal planes (based on magnification); the resulting focal planes were merged into a single, in-focus composite image. Lighting was achieved using an LED illumination dome with all four quadrants set to 99.6% intensity. Scanning electron micrographs of *Euceroptres montanus* Weld were made by the second author and were downloaded for this study from Morphbank (<http://morphbank.net>). All images generated during this study are available under the Morphbank ID 195606.

**Phylogenetic analysis – matrix.**—The matrix used in Buffington et al. (2007) was complemented with the addition of *Ibalia anceps* Say (Ibaliidae). This taxon was included to serve as an additional outgroup to the liopterids (see Ronquist 1999). Sequence data for the ibaliid was downloaded from GenBank (DQ012642, DQ012641, DQ012599, AY621150, EF032242, EF032274). Precisely the same gene regions were used as they were in Buffington et al. (2007); alignments used herein were based entirely on the structural model (Gillespie 2004, Gillespie et al. 2005) proposed for Cynipoidea (Buffington et al. 2007) and included all genetic data; regions of ambiguous alignment were aligned by eye. The model as proposed in Buffington et al. (2007) was not altered by the inclusion of the ibaliid. Morphological and biological characters described in Buffington et al. (2007) were included and used to code *Ibalia anceps*. The final molecular and morphological matrix is available from Treebase (ID SN3726). It should also be noted that Buffington et al. (2007) included a taxon identified as '*Myrtopsen* sp.' from Colombia; this taxon is, in fact, *Scutimica flava* Ros-Farré & Pujade-Villar.

**Phylogenetic analysis – parsimony and Bayesian inference.**—The structurally aligned total evidence matrix was analyzed based on Buffington et al. (2007); the differences are the addition of *Ibalia anceps* in all analyses, and the Bayesian analyses were run for 5 million generations, sampling every 100 generations and burn-in set to 350 (2.5 million generations and burn-in

set to 250 generations in Buffington et al. (2007)).

*List of Depositories.*—

- AMNH American Museum of Natural History, New York, NY, USA.  
 USNM National Museum of Natural History, Washington DC, USA.  
 UCRM Entomology Research Museum, UC Riverside, Riverside, CA, USA.

## DESCRIPTIONS

**Euceroptrinae** Buffington and Liljeblad, new subfamily

Type genus: *Euceroptres* Ashmead, 1896

*Diagnosis.*—The areolet in the fore wing (ARE, Fig. 1D), lack of a hairy ring at the base of the metasoma, lack of a circumtorular impression and well-developed lateral pronotal carina (LPC, Fig. 1A) differentiate this group from Thrasorinae and Plectocynipinae. Nearly all other species of Figitidae have a smooth mesoscutum (save for notauli) whereas the mesoscutum in Euceroptrinae is transversly carinate to rugulose; the only other figitid groups with a transversly carinate mesoscutum are some Aspicerinae (e.g. *Anacharoides* Cameron, *Callaspidia* Dalhöm, *Omalaspis* Giraud and *Pujadella* Ros-Farré) but these species have a sinuate posterior margin of tergum 2 of the metasoma, and are parasites of Syrphidae (Diptera). Parnipinae bears the closest resemblance to Euceroptrinae, but there are several key differences, including the lack of a mesopleural furrow in Parnipinae (complete in Euceroptrinae (F, Fig. 1B)). Parnipinae are Palearctic parasitoids of *Barbotinia* (Cynipidae: Aylacini) on *Papaver* (Papaveraceae) and Euceroptrinae are Nearctic parasitoids of Cynipini (*Andricus* gall inducers) on *Quercus* spp. (Fagaceae) (summarized in Table 1).

*Description.*—Body color black to pale orange; legs orange proximally, darker distally. Female with 12–14 antennal segments; male with 15 segments, first flagellomere laterally excavated. Lateral pronotal

carina (LPC, Fig. 1A) well developed. Mesoscutum ranging from transversly carinate to rugulose; notauli present, well developed; median mesoscutal impression (MMI, Fig. 1C) present, extending up to  $\frac{1}{4}$  length of mesoscutum; scutellum rugulose, posteriorly rounded (Figs 2A–C). Fore wings hyaline, areolet present (ARE, Fig. 1D). Anterior margin of tergum 3 (T3) of metasoma glabrous; T4–T7 with micropores (MP, Fig. 1F) (reduced in some species).

*Euceroptres* Ashmead, 1896: Trans. Am. Entomol. Soc., v. 23, p. 187.

Type species: *Euceroptres primus* Ashmead, 1896 (by monotypy).

Included species: *Euceroptres primus* Ashmead.

*Euceroptres maritimus* Weld, 1926.

*Euceroptres montanus* Weld, 1926.

*Euceroptres whartoni* Buffington & Liljeblad, new species.

*Diagnosis.*—Differs from nearly all other Figitidae by the presence of the areolet in the fore wing (Fig. 1D); the only other group of Figitidae with an areolet is *Parnips* (Parnipinae), but this group lacks a mesopleural furrow. The presence of a well-developed lateral pronotal carina is a plesiomorphic trait within Cynipoidea (Ronquist 1995b, 1999 Ronquist and Nieves-Aldrey 2001, Fontal-Cazalla et al. 2002, Buffington et al. 2007, Liu et al. 2007), and this trait is useful for separating *Euceroptres* from other figitids; among the figitids with this character is *Parnips* (Ronquist and Nieves-Aldrey 2001), all Aspicerinae except *Melanips* (Buffington et al. 2007) and some members of the *Gronotoma* group of Eucoilinae (Fontal-Cazalla et al. 2002, Buffington et al. 2007). Aside from *Parnips*, none of these aforementioned taxa are reared from cynipid galls but are instead reared from cyclorrhaphous Diptera (Ronquist 1999, Buffington et al. 2007). Further, Eucoilinae all possess a scutellar plate with a glandular release pit and nearly all Aspicerinae (except *Melanips*) have a sinuate posterior margin of T-3 of the metasoma (Ronquist 1999, Buffington et al. 2007).

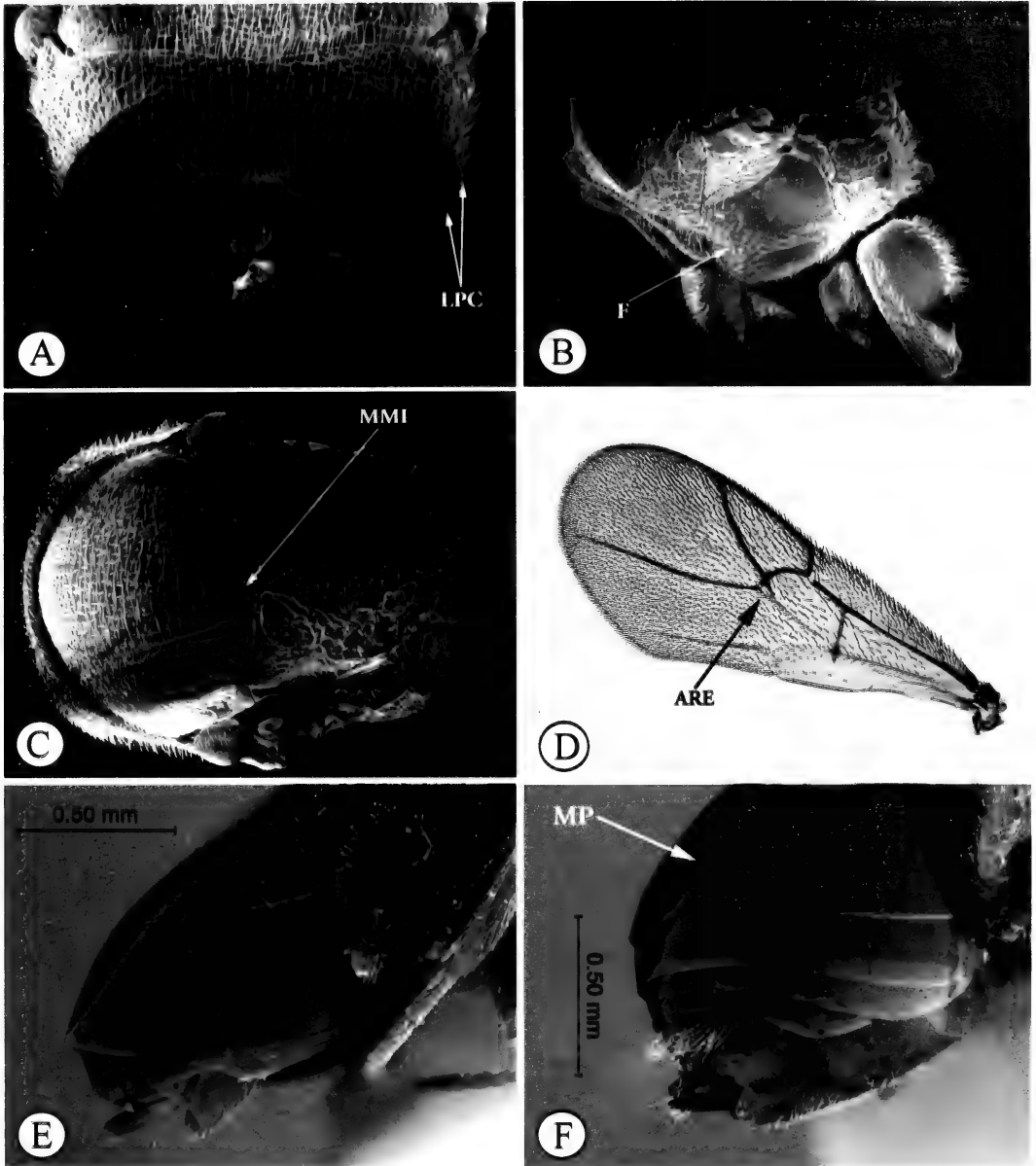


Fig. 1. A–C, F: *Euceroptres montanus* Weld; D: *E. maritimus* Weld; E: *E. whartoni* n. sp. A, mesosoma, anterodorsal view; B, mesosoma, lateral view; C, mesosoma, dorsal view; D, forewing, dorsal view; E–M, female metasoma, posterolateral view. Abbreviations: LPC, lateral pronotal carina; F, mesopleural furrow; MMI, median mesoscutal impression; ARE, areolet; MP, micropore.

**Redescription.—Female. Head.** Black to rusty orange; frons rugulose, densely setose; malar space costulate ventral of eye, rugulose approaching mandibular base; gena and vertex costulate, covered in short appressed setae (Fig. 2A–D); gena

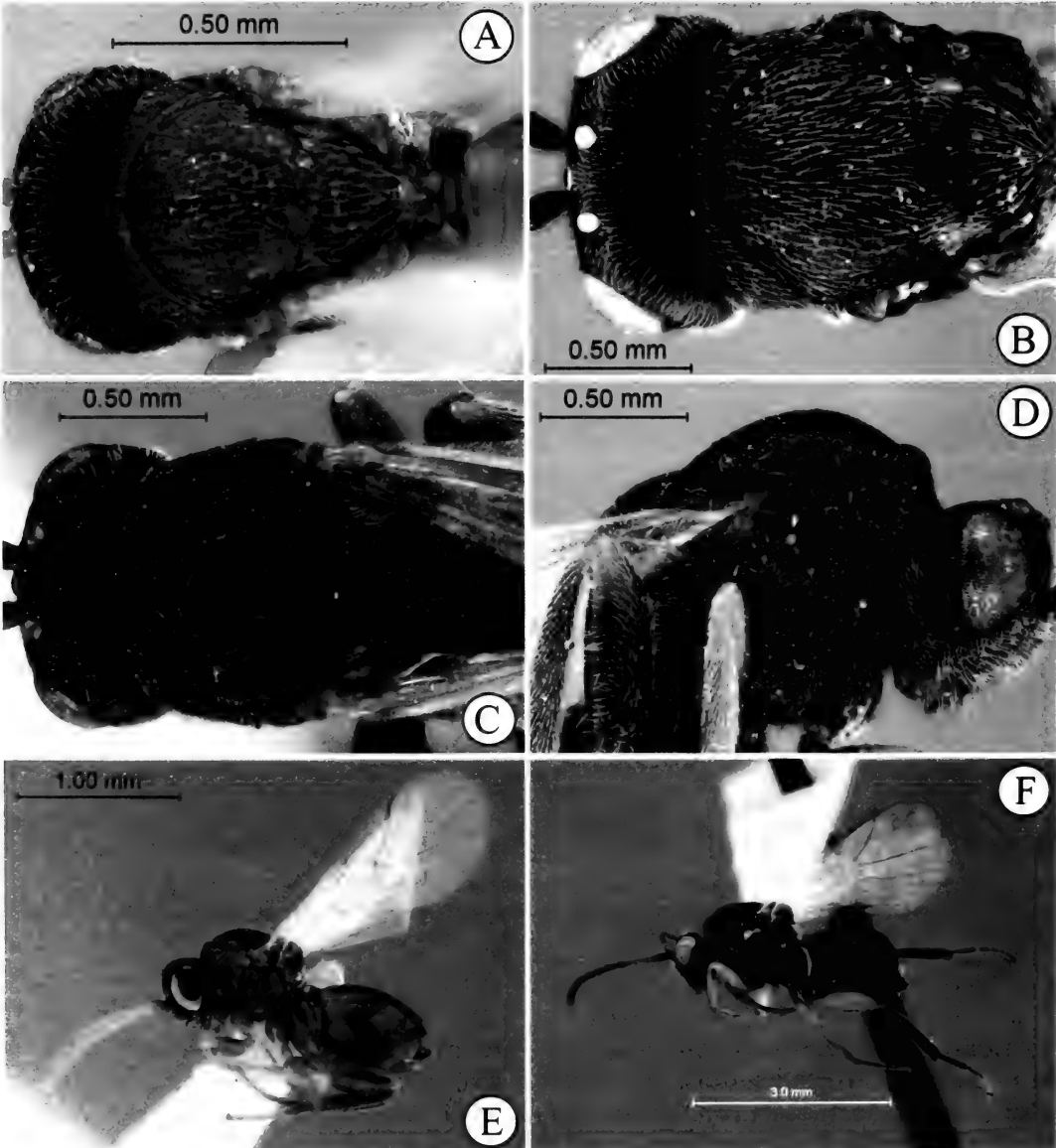
broadly rounded (Fig. 2A–C). Antenna basally orange, distally ranging from orange to dark brown, non-clavate; scape 2.25–3× length of radicle, short appressed setae on all flagellomeres, 10–12 flagellomeres present, moniliform (Fig. 2E–F);



Table 1. Species of *Euceroptres*, their gall wasp hosts and oak hosts.

| <i>Euceroptres</i>  | <i>Andricus</i> gall wasp host   | Oak host species and section  |
|---------------------|--|---|
| <i>E. maritimus</i> | <i>A. quercussuttoni</i>   | <i>Q. agrifolia</i> , <i>Erythrobalanus</i>   |
| <i>E. montanus</i>  | <i>A. truckeensis</i>  | <i>Q. chrysolepis</i> , <i>Protobalanus</i>   |
| <i>E. primus</i>    | <i>A. quercusflocci</i> , <i>A. quercusfutilis</i>                         | <i>Q. alba</i> ( <i>Q. stellata</i> ), <i>Quercus</i>                                       |
| <i>E. whartoni</i>  | <i>A. quercusoperator</i><br>( <i>A. quercuspetiolicola</i> ) <sup>1</sup> | <i>Q. nigra</i> , <i>Erythrobalanus</i><br>( <i>Q. alba</i> , <i>Quercus</i> ) <sup>1</sup> |

1. Dubious host record



A and E: *Euceroptres primus* Ashmead; B and F: *E. maritimus* Weld; C and D: *Euceroptres whartoni* n. sp. A–D, mesosoma, dorsal view; D, mesosoma, lateral view; E–F, habitus, female.

apical segment 2× length of subapical segment.

**Mesosoma.** Lateral surface of pronotum deeply rugulose, densely covered in stiff, moderately long setae (Fig. 1A–B); lateral pronotal carina (LPC, Fig. 1A) well developed, extending from lateral margin of pronotal plate to ventral margin of anteroventral inflection of pronotum (Fig. 1A); lateral margins of pronotal plate indistinct; submedial pronotal depressions deep, open laterally (Fig. 1A). Mesopleuron costulate to rugulose anteriorly, setose; mesopleural furrow composed of rugae (F, Fig. 1B); mesopleural triangle deeply impressed, setose, clearly defined along all edges (Figs 1B & 2D); area posterior of mesopleural triangle and dorsal of mesopleural furrow highly polished, glabrous (Figs 1B & 2D). Mesoscutum transversely carinate to rugulose, moderate to densely setose; anteroadmedian signum present; median mesoscutal impression present, ranging from short, notch-like to ¼ length of mesocutum; notauli complete, originating at anterior end of parascutal impression, gradually becoming wider posteriorly (Figs 1C & 2 A–C). Disk of scutellum heavily rugulose, evenly setose (Fig. 2 A–F); scutellar ridge separating scutellar fovea narrow, short; scutellar fovea oval, obliquely angled relative to midline, posterior rim present, center gently rugulose, sparsely setose (Figs 1C & 2A–C).

**Metapleural-propodeal complex.** Metapleuron and propodeum ranging from glabrous to completely covered in long setae; anterior margin of upper metapleural area jutting-out laterally, glabrous (Fig. 1B); setal pit at ventral margin of

metapleuron present; posterior aspects of propodeum smooth to gently rugulose, flat; propodeal carinae thin, complete, parallel; area between propodeal carinae glabrous to setose, with dense, felt-like setae under long, thin setae. Nucha short, glabrous, deeply striate.

**Fore wing.** Marginal cell closed along anterior margin (Fig. 1D); distinct break present in vein proximal to marginal cell (Fig. 1D); areolet present (ARE, Fig. 1D); marginal and cubital veins represented by trace veins; short setae present on wing surface and along margins.

**Legs.** Femora orange, tibiae orange to dark brown; sparse, appressed setae present on all femorae and tibiae. Tarsomeres orange-yellow to brown, covered in short, appressed setae (Fig. 2E–F).

**Metasoma.** Ranging from black or brown to orange; petiole frequently obscured by anterior margin of T3. Posterior margins of T3 and T4 parallel, angled obliquely at 45 degrees relative to horizontal, subequal in length; remaining terga short, telescoped within T4; T4–T9 with micropores (MP, Fig. 1F) though significantly reduced to absent in some species; setae frequently present on T8.

**Male.** As in female but with 13 flagellomeres; flagellomere 1 as long as fourth antennal segment, laterally excavated, expanded slightly on distal end.

**Distribution.** Nearctic Region: United States of America: AZ, CA, DC, FL, MA, MD, OR, TX, VA.

**Biology.** Parasitoids of species of *Andricus* (Cynipidae: Cynipini), which are gall inducers on various species of oak (*Quercus* spp.).

KEY TO SPECIES OF *EUCEROPTRES* (FEMALES AND MALES UNLESS OTHERWISE NOTED)

- 1. Females with 11 flagellomeres. Metasomal terga 3 – 8 with significantly reduced to absent micropores (Fig. 1) (collected East of the Rocky Mountains) . . . . . 2
- Females 10 or 12 flagellomeres. Metasomal terga 3 – 8 with well developed micropores (MP, Fig. 1F) (collected West of the Rocky Mountains) . . . . . 3
- 2. Median mesoscutal impression short, notch-like . . . . . *Euceroptres primus* Ashmead

- Median mesoscutal impression elongate, often 1/4 to 1/3 length of mesoscutum . . .  
   . . . . . *Euceroptres whartoni*, new species
- 3. Females with 10 flagellomeres. Dense, felt-like setae present in mesopleural triangle and  
   setal pits between propodeal carinae (Fig. 1B). Area of episternum posterior to  
   anterodorsal margin of metepisternum gently crenulated . . . *Euceroptres maritimus* Weld
- Females with 12 flagellomeres. No felt-like setae present. Area of episternum posterior  
   to anterodorsal margin of metepisternum smooth and glabrous . . . . .  
   . . . . . *Euceroptres montanus* Weld

### *Euceroptres maritimus* Weld, 1926

Figs 1D & 2B, F

**Diagnosis.**—Females readily distinguished by having 10 flagellomeres (all other species with either 11 or 12). Separated from *E. primus* and *E. whartoni* by the presence of well-developed micropores on the metasoma (cf. MP, Fig. 1F); this trait is also shared with *E. montanus*. Males and females have dense felt-like setae present in the mesopleural triangle, the setal pits of the metapleuron and between the propodeal carinae; all other species have setae in these areas, but they are not dense and felt-like.

**Redescription.**—**Female.** As in description of genus, with antennae of female 12 segmented (10 flagellomeres); median mesoscutal impression deep, short, notch-like (Fig. 2B); mesoscutum distinctly transversely rugulose across entire surface; dorsal-anterior margin of mesopleuron umbilicate-rugulose, transitioning to rugulose ventrally; mesopleural triangle with dense, felt-like setae; metapleuron evenly covered with long setae except episternal area posterior to anterior impression of metepisternum, smooth, glabrous; felt-like setae in ventral setal pit; metasomal T4–T9 with distinctly visible micropores (cf. Fig. 1F), dense setal band present along posterior margin of T8; metafemora orange; metatibia medially orange, laterally dark brown; pro- and mesotarsomeres dark orange to brown; metatarsomeres dark brown or black.

**Male.** As in female but with 13 flagellomeres; flagellomere 1 as long as fourth

antennal segment, laterally excavated, expanded slightly on distal end.

**Material examined.**—Holotype. [first label] “Berkeley, Calif 4/20/12” [20 April 1912], [second label] “Mrs. G.D. Louderbeck”, [third label] “1601”, [fourth label] “*Quercus agrifolia*”, [fifth label] “Type 27299, U.S.N.M.”, [sixth label] “*Euceroptres maritimus* Weld”. The holotype is a female in good condition, deposited in the USNM. **Additional material.** Allotype. Same data as holotype, 1 male (USNM). Paratypes. USA: CALIFORNIA. **Alameda Co.** Same data as holotype, 1 female; Oakland. Bred by Bassett from galls collected by W.M. Beutenmueller, Beutenmueller Coll., received 1935 [no other data available], 1 male (USNM). **Los Angeles Co.**, Santa Anita, Hopkins File number 15605 $\frac{5}{6}$ , June 17–18 1918, reared from *Quercus agrifolia*, collected and bred by L. Weld, 1 female (USNM). **Alameda Co.**, ‘through C.V. Riley’, [no other data available], 4 males, 3 females (USNM). Non-types. USA: CALIFORNIA. **Alameda Co.**, Berkeley, gall collected 10 Mar 1928 from *Quercus agrifolia*, emerged 15 May 1928, W. Ebeling, coll., 3 males, 3 females (AMNH). **Los Angeles Co.** Pasadena, gall collected 22 Feb 1920 from *Quercus agrifolia*, Kinsey Coll., ex gall of *Callirhytis polythra* Bassett, 23 males, 46 females (AMNH); Claremont, Metz Coll., acc 5635 [no other data available], 1 male (AMNH); Eaton Canyon State Park., 19.IV.2004, ex gall on *Quercus agrifolia*, M. Buffington & J. Liljeblad, 12 males and 15 females (1 male, 1 female under voucher 56737, UCRM; remaining specimens in USNM). OREGON. **Josephine Co.**, Grants Pass, coll #8536, taken from *Quercus* spp., [no other data available], 5 males, 13 females (AMNH).

Note: Weld (1926) recorded that part of the paratype series was sent to the USNM under the Hopkin’s number 15605 $\frac{5}{6}$ , which was supposedly collected in Montecito, CA

(near Santa Barbara); the specimen in USNM bearing this Hopkin's number is labeled as being collected in Santa Anita, CA (near Pasadena), not Montecito.

**Distribution.**—Western United States, from southern Oregon in the north to southern California in the south.

**Biology.**—Reared from the cynipid *Andricus quercussuttoni* (Bassett) on *Quercus agrifolia* Née.

***Euceroptres montanus* Weld, 1926**

Fig. 1A–C, F

**Diagnosis.**—Females readily distinguished from other *Euceroptres* species by the possession of 12 flagellomeres. Males can be distinguished from *E. maritimus* and *E. primus* by having the area of the episternum posterior of the anterodorsal margin of the metepisternum smooth and glabrous (gently crenulate and setose in *E. maritimus* and *E. primus*); from males of *E. whartoni* by the umbilicate anterodorsal margin of the mesopleuron (rugulose in *E. whartoni*), and the presence of micropores on T4–T9 (present but barely visible in *E. whartoni*).

**Redescription.**—**Female.** As in description of genus, with antennae of female with 12 flagellomeres; median mesoscutal impression deep, short, notch-like (Fig. 1C); mesoscutum distinctly transversely rugulose across entire surface; dorsal-anterior margin of mesopleuron umbilicate, transitioning to rugulose ventrally; mesopleural triangle setose; metapleuron evenly covered with long setae, with denser setae in ventral setal pit; metasomal T4–T9 with distinctly visible micropores (cf. Fig. 1F), dense setal band present along posterior margin of T8; metafemora and metatibiae orange; pro-, meso- and metatarsomeres dark orange to brown.

**Male.** As in female but with 13 flagellomeres; flagellomere 1 as long as fourth antennal segment, laterally excavated, expanded slightly on distal end.

**Material examined.**—Holotype. [first label] "Idyllwild, Cal.", [second label] "1622", [third label] "Type No. 27228 U.S.N.M.", [fourth label] "*Euceroptres montanus* Weld". The type is a female in good condition, deposited in USNM. **Additional material.** Allotype. USA: CALIFORNIA. **Riverside Co.** Idyllwild, April [19]23 (remaining label data as in holotype labels), 1 male (USNM). Paratypes. USA: CALIFORNIA. **Riverside Co.** Idyllwild, April [19]23 (remaining label data as in holotype labels), 17 males, 19 females (USNM). **Trinity Co.** Big Bar, cut out Dec [19]23, code 1622, 1 female (USNM). **El Dorado Co.** Kyburz, code 1622 [no other data available], 1 female (USNM). **OREGON. Douglas Co.** Canyonville, June 3 [no year recorded], code 1622, Beut.[enmueller] Coll., rec'd 1935, 2 males, 4 females (USNM). **Josephine Co.** Holland, April [19]23, code 1622, 1 male (USNM). Non-types. USA: CALIFORNIA. **Santa Clara Co.** Los Gatos, Hopkin's number 15922<sup>2</sup>, reared various dates between 7–21 May 1919 from *Quercus chrysolepis* Liebm., R.D. Hartman, collector, 5 males, 4 females (USNM).

Note: Weld (1926) recorded two specimens of this species recorded from Kern Co., CA, from the 'Museum', presumably the USNM; these specimens were not located.

**Distribution.**—Western United States, from southern Oregon in the north to southern California in the south.

**Biology.**—Reared from the cynipid gall inducer *Andricus truckeeensis* (Ashmead) on *Quercus chrysolepis* Liebm. in CA. This data taken from Weld (1926); no specimens were found in the USNM with associated host data.

***Euceroptres primus* Ashmead, 1896**

Fig. 2A & 2E

**Diagnosis.**—Females distinguished from *E. montanus* and *E. maritimus* by possessing 11 flagellomeres (12 in *E. montanus*, 10 in *E. maritimus*) and lacking micropores on metasomal T4 through T9 (males and females). *Euceroptres whartoni* also has 13 antennal segments in the female, but *E. primus* can be separated from *E. whartoni* by the short median mesoscutal impression

(elongate,  $1/4$ – $1/3$  length of mesoscutum in *E. whartoni*; compare Fig. 2A with 2C) in both males and females; *E. primus* also lacks micropores on metasomal T4–T8 (faintly visible in *E. whartoni*).

**Redescription.**—**Female.** As in description of genus, with antennae of female with 11 flagellomeres; median mesoscutal impression deep, short, notch-like (Fig. 2A); mesoscutum distinctly transversely rugulose across entire surface; dorsal-anterior margin of mesopleuron gently rugulose, setose; mesopleural triangle setose; metapleuron evenly covered with long setae, anterior margin of episternum gently rugulose, occasionally glabrous; dense setae in ventral setal pit; metasomal T4–T9 without visible micropores (cf. Fig. 1E), dense setal band lacking along posterior margin of T-8 (cf. Fig. 1E); metafemora and metatibiae orange; pro-, meso- and metatarsomeres dark orange to brown.

**Male.** As in female but with 13 flagellomeres; flagellomere 1 as long as fourth antennal segment, laterally excavated, expanded slightly on distal end.

**Material examined.**—For the purposes of nomenclatural stability, the female specimen in the USNM, currently labeled 'type #3286' is designated as lectotype. Lectotype. [first label] "Through C.V. Riley", [second label] "2640, scrub oak, Whitfelt, Georgiana, Fla., Mar 24 – [18]82, [third label] "Type No. 3286, U.S.N.M., [fourth label] '*Euceroptres primus* Ashm.'", [fifth label] Lectotype designation. The lectotype is a female in good condition, deposited in USNM. **Additional material.** Paralectotypes. USA: FLORIDA. **Brevard Co.** Georgiana, through C.V. Riley, 2640, scrub oak, Whitfelt, Georgiana, Fla., Mar 24 – [18]82, 1 male (USNM) [this specimen was included in Ashmead's original description]; Georgiana, through C.V. Riley, 2640, scrub oak, Whitfelt, Georgiana, Fla., Mar 7 – [18]82, 1 female (USNM). MASSACHUSETTS. Merrimac River, "780P", through C.V. Riley, 3 July, 1883, ex *Quercus alba* L., 2 females (USNM). Non-types. USA: VIRGINIA. **Fairfax Co.** Falls Church, Minor's Hill, Hopkin's number 8489<sup>2</sup>, reared 24 Jun – 11 Jul 1912, ex *Quercus alba* L. Wm. Middleton, collector, 5 males, 7 females

(USNM); Falls Church, Hopkin's number 8489<sup>5</sup>, reared 24 Jun 1912, ex *Quercus alba* L., Wm. Middleton, collector, 4 males (USNM); Falls Church, Hopkin's number 8491<sup>2</sup>, reared 29 Jun 1912, ex galls of *Callirhytis papillatus*, Wm. Middleton, collector, 4 males, 4 females (USNM); Falls Church, Hopkin's number 12059, reared 25 Jun 1914, ex *Quercus alba* L., Wm. Middleton, collector, 1 male (USNM); Falls Church, Kearney, Hopkin's number 12069<sup>2</sup>, reared 27 Jul 1914, ex *Quercus minor* (Marshall) Sarg., Wm. Middleton, collector, 1 male (USNM); Falls Church, Hopkin's number 13600, reared 26 Apr 1915, ex galls of *Andricus flocci*, Wm. Middleton, collector, 4 males (USNM); Falls Church, Kearney, Hopkin's number 12069<sup>2</sup>, reared 27 Jul 1914, ex *Quercus minor* (Marshall) Sarg., Wm. Middleton, collector, 1 male (USNM).

**Distribution.**—Eastern United States, from Maryland in the north to Florida in the south.

**Biology.**—Reared from *Andricus quercus-futilis* (Osten-Sacken) and *Andricus quercus-flocci* (Walsh) on *Quercus alba* L.; also reared from an unknown cynipid host on *Quercus stellata* Wangenheim. Weld (1926) also records this species from petiole galls on *Quercus stellata* from Rosslyn, VA but these specimens could not be located in the USNM.

***Euceroptres whartoni* Buffington &  
Liljeblad, new species**  
Figs 1E & 2C–D

**Diagnosis.**—Females can be distinguished from *E. montanus* and *E. maritimus* by the possession of 11 flagellomeres (12 in *E. montanus*, 10 in *E. maritimus*) and the lack of distinct micropores on metasomal T4 through T9 (Fig. 1E) (males and females); distinguished from *E. primus* by the presence of an elongate median mesoscutal impression (short and notch-like in *E. primus*; viz. Fig. 2A & 2C).

**Description.**—**Female.** As in description of genus, with antennae of female with 11 flagellomeres; median mesoscutal impression deep, elongate, reaching  $1/4$  to  $1/3$  length of mesoscutum (Fig. 2C); mesoscu-

tum distinctly transversely rugulose anteriorly, less striate posteriorly; dorsal-anterior margin of mesopleuron shagreen to gently rugulose, setose; mesopleural triangle setose; metapleuron evenly covered with long setae, anterior margin of episternum gently rugulose, frequently glabrous; dense setae in ventral setal pit; metasomal T4–T9 without visible micropores (Fig. 1E), dense setal band lacking along posterior margin of T8 (cf. Fig. 1E); metafemora and metatibiae orange; pro-, meso- and metatarsomeres dark orange to brown.

**Male.** As in female but with 13 flagellomeres; flagellomere 1 as long as fourth antennal segment, laterally excavated, expanded slightly on distal end.

**Etymology.**—Named in honor of our mentor and friend, Robert Wharton.

**Material examined.**—Holotype. [first label] Hopk. U.S. 10767<sup>s</sup>, [second label] reared Mar. 26.21 [26 Mar 1921], *Quercus minor*, [fourth label] Denton, TX, [fifth label] Marquis, R.L., coll., [sixth label] holotype, *Euceroptres whartoni* Buffington & Liljeblad. The holotype is a male in good condition, deposited in the USNM. **Additional material.** Paratypes. Same data as holotype: USA: TEXAS. **Denton Co.** Denton, ex triangular galls on *Quercus minor*, collected 26 Jan 1920 [emergence date not recorded], R.L. Marquis, collector, Hopkin's number 10767<sup>s</sup> (2 males and 4 females, NHMN). Non-types. USA. **FLORIDA. Volusia Co.** Hopkin's number 15634g, reared 15 Oct 1922 from woolly midrib cluster galls collected 8 Dec 1919 from *Quercus laurifolia* Michx. (1 female, NMHH). **MARYLAND. Montgomery Co.** Plummers Island, 12 Apr 1914, W.L. McAtee, coll. (1 male, USNM). **MISSOURI. Stoddard Co.** 30 Mar 1938, T-10242, on peach (1 female, USNM). **VIRGINIA. Fairfax Co.** East Falls Church, Hopkin's number 13651i, 23 Apr 1917, reared from *Callirhytis operator* sexual generation [in Weld's hand] collected from *Quercus marylandica* Du Roi, Wm. Middleton, coll., 1 Jun 1916 (2 females, USNM). [collection data unknown] No. 2640, Apr 19.82 [(19 Apr 1882(?)), (1 male USNM); No. 2640, Apr 21.82 [(21 Apr 1882(?)), (1 male USNM); [collection data unknown] "with *A. cicatricula* Bass." [this specimen corresponds to a specimen mentioned in Weld (1926), originally

determined as *E. primus*, that was originally found among the cotype material of *Cynips cicatricula* Bassett, collected from *Quercus alba* in Waterbury, CT.] (1 male, USNM).

**Distribution.**—Eastern and Southeastern United States, from Texas in the West to Connecticut and Maryland in the East.

**Biology.**—Reared from *Andricus quercus-operator* (Osten-Sacken) galls on *Quercus nigra* L. in Virginia. A second rearing record is circumstantial at best: specimens mentioned above that were associated with *Cynips cicatricula* Bassett (= *Andricus quercuspetiolicola* (Bassett)) were bred from *Quercus alba* L. *Quercus nigra* and *Q. alba* belong to different sections of *Quercus* subg. *Quercus*; the former is a red oak whereas the latter is a white oak. Not much is known about the host-specificity of *Euceroptres*. If they are anything like the cynipid inquiline or even true parasitoids, these host records could very well be correct. On the other hand, no Nearctic species of oak gall wasps is known to attack hosts from more than one oak section (Stone et al. 2002).

## DISCUSSION

Two distinct lineages of *Euceroptres* emerged from this study. One, composed of *E. maritimus* and *E. montanus*, appears to be restricted to the western Nearctic Region, chiefly collected in CA and OR. The second lineage comprises *E. primus* and *E. whartoni* and occurs in the eastern and southeastern Nearctic Region. In fact, this latter lineage may be rather widespread throughout the southeast. Within *Euceroptres*, based on characters described herein, the following set of relationships is proposed: ((*E. montanus* + *E. maritimus*) (*E. primus* + *E. whartoni*)). The first clade (*E. montanus* + *E. maritimus*) is united by the shared presence of micropores on the metasoma (Fig. 1F) and a distribution restricted to the western Nearctic. The second clade, composed of (*E. primus* + *E. whartoni*) are united by the shared presence of 13 antennal segments in the female, the overall reduction in micro-

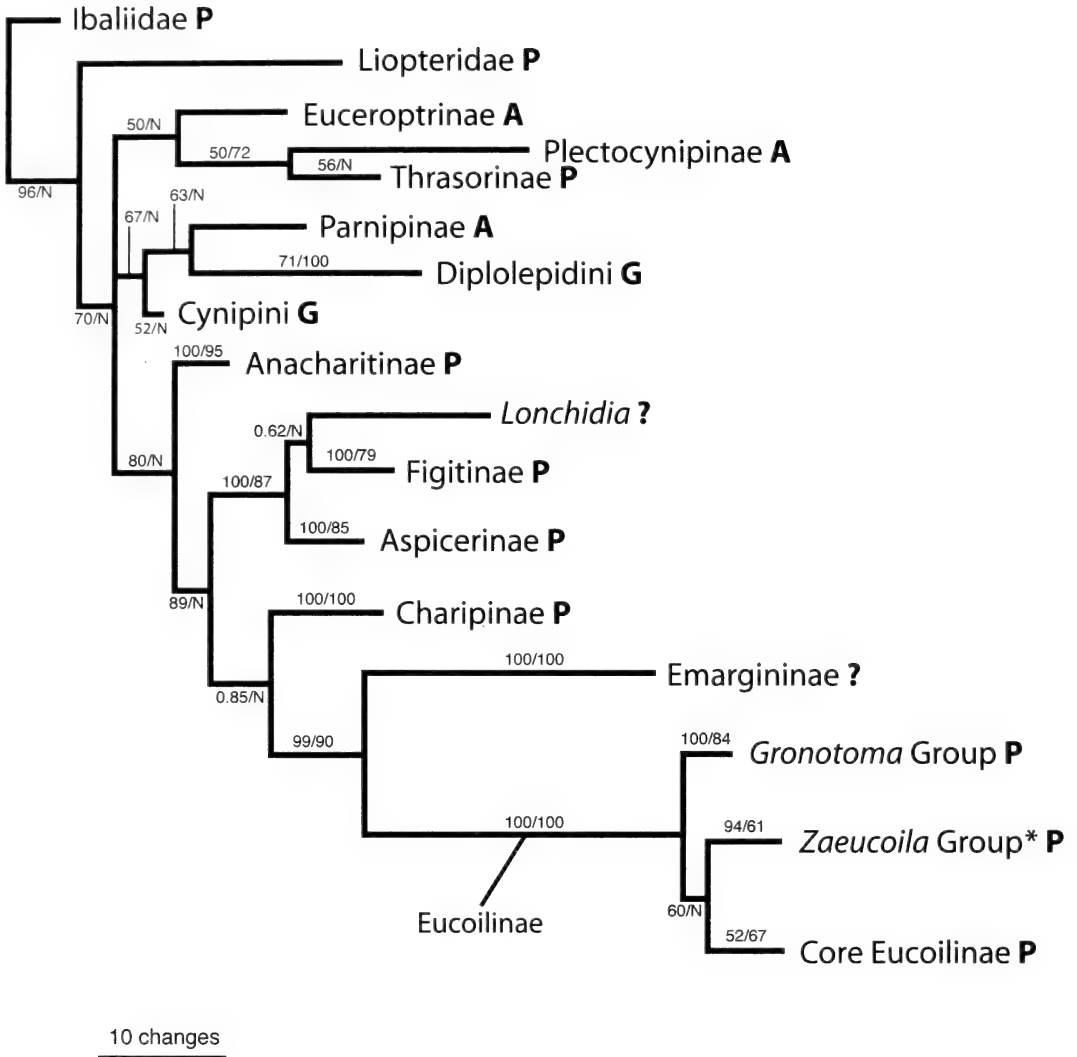


Fig. 3. Phylogram of Figitidae resulting from Bayesian analysis of 28S D2&D3 and 18S rRNA, COI and morphology (see *Materials and Methods*). Analyses of the same data using parsimony result in nearly the same tree (see below); '\*' at the *Zaeucoila* Group indicates this clade is sister-group to the *Gronotoma* group in the parsimony analysis. Letters after terminal names refer to: A, agastoparasite; G, gall inducer; P, non-agastoparasite. Numbers on branches indicate branch support in the form of Bayes posterior probability/ parsimony bootstrap support; 'N' indicates less than 50% support was recovered for that node; Bayesian posteriors calculated using 50% majority rules consensus. Parsimony analysis resulted in 375 trees distributed across 46 islands; CI=.18, RI=.62.

pores on the metasoma, and a distribution encompassing the eastern/southeastern Nearctic Region.

A striking symplesiomorphy of *Euceroptres* is the presence of a very well developed lateral pronotal carina (Fig. 1A). As stated earlier, this character is shared with *Liopteridae* (Ronquist 1995b) and *Stolamidae*

(Liu et al. 2007), the figitids *Aspicerinae*, *Parnipinae*, the *Gronotoma* group of *Eucoilinae* (Buffington et al. 2007) and a few *Cynipidae* (Ronquist 1995b).

Conclusive evidence for the exclusion of *Euceroptres* from *Thrasorinae* was provided in two independent studies (Ros-Farre and Pujade-Villar 2007, Buffington et al. 2007)



as well as this study (Fig. 3). With the erection of Euceroptinae, a system of small subfamilies, sister to the remaining higher taxa within Figitidae, reflects a rather complicated evolutionary history (Fig. 3). It should be noted, however, that the branch support for (Euceroptinae (Plectocynipinae+Thrasorinae)) is weak in both parsimony and Bayesian analyses (Fig. 3). As stated by Buffington et al. (2007), additional data are required to definitively resolve these relationships; data collection for additional species of Plectocynipinae and Thrasorinae is currently underway (Buffington and Scheffer unpublished).

The association of these lineages with gall-inhabiting hymenopterous hosts begs the intriguing possibility that phytophagous cynipids arose from a rather diverse range of proto-figitids attacking various gall-inducing hosts (Ronquist and Nieves-Aldrey 2001). These lineages also may represent the origins of agastoparasitism within Cynipoidea, though Nylander (2004) and Melika (2006) suggest inquilinism arose independently in Cynipidae numerous times. Certainly within Figitidae, agastoparasitism is the plesiomorphic life-history strategy (Fig. 3, terminals lettered 'A', agastoparasites; 'G', gallers; 'P', non-agastoparasites), with the more derived Thrasorinae shifting to chalcidoid hosts (Ros-Farré and Pujade-Villar 2007, Buffington et al. 2007, Buffington submitted).

Although the cynipid hosts of *Euceroptres* gall only 5 or 6 species of *Quercus*, their oak hosts could hardly be a more diverse sample coming from the Nearctic (Table 1). All three sections of *Quercus* subgenus *Quercus* are represented, the missing fourth being the exclusively Palearctic section *Cerris* (Manos et al. 1999). This could be just a random sample from a few species attacking a number of *Andricus* gall wasps. If, however, species of *Euceroptres* are more host-specific, it lends further support to the idea that this genus was once a more

species rich group of which only a few scattered lineages have survived to date. Liu et al. (2007) date the split of cynipids and figitids to at least the early Cretaceous, providing evidence that even 'neo-eucoilines' ('core' Eucoilinae of Fontal-Cazalla et al. 2002; *Zamischus* group of Buffington et al. 2007) were present in the mid-Cretaceous. These data suggest the Figitidae are indeed an old lineage, and members of these depauperate ancestral lineages may represent so-called 'living fossil' taxa, giving us a tantalizing opportunity to look into the evolutionary history of this diverse group of parasitoid Hymenoptera.

## ACKNOWLEDGMENTS

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## Load Carriage during Foraging in Two Species of Solitary Wasps

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**Abstract.**—Foraging strategies of two species of solitary digger wasps (Hymenoptera: Crabronidae) were examined. Both species capture insects and return with them in flight to a burrow where they are used as food for larvae. The actual loading of the wasps was compared to a theoretical ideal, the maximum that they should be able to carry in flight. *Bembix troglodytes* Handlirsch is a relatively large wasp that carries many small flies to its burrows. The flies are much smaller than the ideal size, but the choice of small prey appears to be adaptive in that it should reduce the rate of stealing of flies by conspecific females, which was a common event. *Tachytes chrysopyga* Cresson is a relatively small wasp that carries relatively large prey, grasshoppers and crickets, to its burrow. The average size of prey appears to be ideal; however, the distribution of prey size is so great that many wasps were underloaded, while others were overloaded. Prey theft was not observed in *T. chrysopyga*, and flexible flight behaviors (e.g. short, hopping flights) allow it to carry a broad range of prey sizes. These two wasp species may represent near extremes of a continuum of behavior among predaceous wasps.

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Although much is now known about the foraging and nest provisioning behaviors of solitary wasps (O'Neill 2001, Evans and O'Neill 2007), their foraging strategies have not been extensively studied using the conceptual framework offered by optimal foraging theory. One approach to examining foraging decisions in such species is to develop a prediction of the optimal load size of the prey, and to test this prediction against the size of actual loads. Fortunately, the maximal load size is simple to calculate for species that carry the prey in flight. Marden (1987) measured the maximum lift force of a variety of flying animals, including 33 bees and wasps, by progressively loading individuals with weights until they could not take off. The force production of flying animals is primarily dependent on their flight muscle mass. In Hymenoptera, this relationship is quite strong ( $r^2 = 0.99$ ), and at the

maximum load mass, the ratio of flight muscle mass to body mass (or flight muscle ratio, FMR) is 0.179 (Marden 1987).

Use of flight muscle ratio as a metric for flight capability has several advantages, primarily its independence of the size of the wasp. For wasps that carry their prey in flight, the maximum force produced must equal or exceed the combined weight of the wasp and prey. Assuming it is optimal for a wasp to carry the largest prey possible, the FMR (now flight muscle mass divided by combined body and prey mass) should approach but not exceed 0.179. We have tested this prediction in yellowjackets (*Vespula* spp, Coelho and Hoagland 1995), the eastern cicada killer (*Sphecius speciosus* Drury, Coelho 1997), the great golden digger wasp (*Sphex ichneumoneus* L., Coelho and LaDage 1999), and the carpenter wasp (*Monobia quadridens* L., Edgar and Coelho 2000). In no case yet examined has

the FMR of foraging wasps fallen precisely at the predicted value; however, investigation of the causes for the deviation from "optimality" has always revealed interesting insights into foraging behavior. In this study we apply this method to examine the foraging strategies of two rather different crabronid wasps facing different selection pressures.

### *Bembix*

The general biology of *Bembix* and specific details of *B. troglodytes* Handlirsch, the subject of this study, are described by Evans (1957; 1963). Only relevant aspects of their behavior are summarized here. *Bembix* is a genus of crabronid wasps that hunt flies (Diptera) and carry them to their burrow in flight. The female digs a single burrow in the ground and excavates a nest cell. In progressive provisioners, an egg is laid and attached to the first prey in the cell or to the substrate in the center of the cell. In *B. troglodytes*, oviposition occurs in an empty cell, and the first fly is captured, paralyzed and placed in the cell later (Evans 1957, Evans and O'Neill 2007). The female continues to capture flies and feed them to its developing larva. As the larva increases in size, the rate of provisioning increases (Tengö et al. 1996). A final flurry of foraging provides the larva with all the flies it will require and the female then seals the burrow and digs another. *Bembix* burrows often occur in high-density aggregations, perhaps as a response to parasite and predator pressure, as the relative incidence of parasites per nest decreases with increasing nest density in at least one species (Larsson 1986). *Bembix troglodytes* females close the burrow when leaving it to hunt, but only when the larva is young. The burrow is left open during the intensive foraging phase and closed only at night. *Bembix* exploit the most abundant flies available, apparently learning the richest sources of flies and repeatedly exploiting them (Evans 1957, 1963). *Bembix troglodytes* preys upon a large variety of

flower-visiting flies, though most are relatively small in size. Exceptionally small flies are provided to young larvae, while older larvae are provisioned with larger flies. Digging and provisioning a single nest requires only about six days and from 21 to 26 flies are required to fully provision a larva (Evans 1957).

### *Tachytes*

*Tachytes* is a genus of digger wasps that stocks its underground burrows with Orthoptera carried in flight from foraging areas. *Tachytes* digs complex burrows with multiple cells and packs each cell with up to 10 prey items. The egg is not laid until the cell is fully provisioned (Evans and Kurczewski 1966, Elliot and Salbert 1981), a case of mass provisioning. *Tachytes* nest aggregations are sometimes associated with those of *Sphecius*, as they were in this study. In one species, *T. distinctus* F. Smith, males establish perches near the nest entrance of a female and chase any insect that flies near, including brood parasites such as *Zanysson texanus* (Cresson) (Lin and Michener, 1972).

## MATERIALS AND METHODS

We conducted our observations and measurements on a large nesting aggregation of *Bembix troglodytes* Handlirsch at the Hot Springs area of Big Bend National Park (N 29° 10' 39.57" latitude, W 102° 59' 52.73" longitude, Brewster Co., Texas) from 22 to 23 May 2006. We noted other aggregations, apparently of the same species, at Santa Elena Canyon and Boquillas Canyon, all in sandy areas immediately adjacent to the Rio Grande River. These aggregations were in approximately the same locations as those we observed in previous years. Female wasps carrying prey were netted and weighed on an Ohaus Adventurer-Pro electronic balance to the nearest mg. The head, abdomen, legs and wings of the wasps were removed with scissors and the thorax mass determined. Flight muscle mass was estimated

as 95% of thorax mass (Marden 1987). The mass of the prey fly and its thorax mass were similarly determined. Several of the wasps were collected as voucher specimens and deposited in the Lafayette College Insect Collection and the Quincy University Life Sciences Museum.

We discovered a large colony of *Tachytes chrysopyga obscurus* Cresson nesting on an earthen berm within an even larger aggregation of the eastern cicada killer (*Sphecius speciosus* Drury). This berm was located within a large chemical production facility (Flint Hills Resources) in Will County, IL, at N 41° 26' 39.31'' latitude, W 88° 10' 22.16'' longitude. From 27 to 28 July, 2006, female wasps were collected as they returned to their burrows with prey. Body, thorax and prey mass were determined as described above. Several wasps were collected as voucher specimens and deposited with the California Academy of Sciences entomology collection. All prey were deposited in the Quincy University Life Sciences Museum. All data are reported as mean  $\pm$  standard error unless otherwise indicated. Descriptive statistics were calculated using Microsoft® Excel 2003, while *T* tests were performed using VassarStats (Lowry 2007).

## RESULTS

### *Bembix troglodytes*

*Bembix troglodytes* females averaged  $99 \pm 2$  ( $N = 48$ ) mg in body mass and  $37 \pm 0.003$  ( $N = 48$ ) mg in thorax mass, resulting in an unladen FMR of  $0.36 \pm 0.004$  ( $N = 48$ ). Fly prey of *B. troglodytes* averaged  $45 \pm 3$  ( $N = 33$ ) mg in body mass and  $16 \pm 1.1$  ( $N = 33$ ) mg in thorax mass, resulting in an FMR of  $0.33 \pm 0.01$  ( $N = 32$ ). Carrying flies resulted in a loaded FMR of  $0.29 \pm 0.006$  ( $N = 27$ ) for female *B. troglodytes* and loaded FMR ranged from 0.23 to 0.34. Hence, all fly-carrying females had FMRs well above the marginal FMR of 0.179 (Fig. 1A).

There was no significant relationship between wasp body mass and prey body

mass in *B. troglodytes*. However, small wasps were restricted to the smallest flies, while larger wasps carried a greater range of sizes of flies (Fig. 2A).

There were usually many wasps flying about the nest aggregation, some of which were doubtlessly males engaged in the sun dance (Evans 1957). Many, however, were females. As successful hunters returned to the aggregation, they were nearly always pounced upon by conspecifics before they had the opportunity to land. Often the prey was dropped, and then picked up by the same or another female. Prey-laden females were fast, maneuverable, surprisingly difficult to distinguish from unladen females, and difficult to catch. The fly was tucked under the body and held tightly with all legs. A slightly larger profile normally provided the investigator with the cue that a wasp was carrying prey. *Bembix troglodytes* with prey generally landed and entered their burrows very rapidly if they escaped attempts at prey theft.

Digging activity was frequent. The thistledown velvet ant (*Dasymutilla gloriosa* (Sauss.)), a brood parasite, was common in the area, and often observed digging in the sand as well as entering open burrows. Brood parasitic satellite flies were frequently observed perched at nest entrances and occasionally entering burrows, sometimes closely following prey-laden *B. troglodytes* down their burrows.

Prey flies collected for this study were dismembered to determine their FMR, and could not be subsequently identified to any great degree.

### *Tachytes chrysopyga*

*Tachytes chrysopyga* females averaged  $52 \pm 2.6$  ( $N = 31$ ) mg in body mass and  $18 \pm 1.0$  ( $N = 31$ ) mg in thorax mass, yielding an unladen FMR of  $0.33 \pm 0.007$  ( $N = 30$ ). Prey items of *T. chrysopyga* averaged  $50 \pm 4.8$  (31) mg, producing a mean loaded FMR of  $0.18 \pm 0.007$  ( $N = 30$ ) in the wasps. The latter value is very close to the

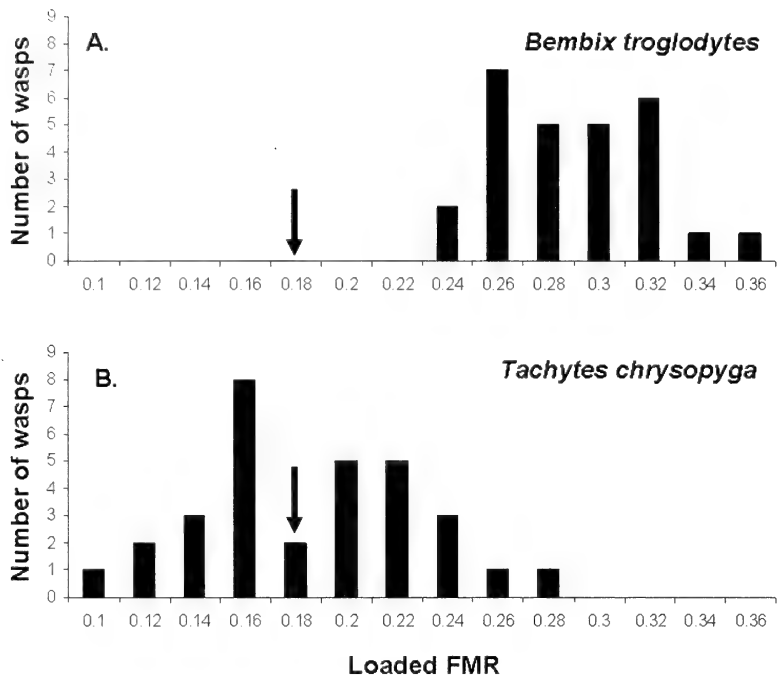


Fig. 1. The distribution of flight muscle ratios (FMR) in wasps carrying prey. Arrows indicate the marginal flight muscle ratio, below which take-off is not possible. a. *Bembix troglodytes* from south Texas. b. *Tachytes chrysopyga obscurus* from northern Illinois.

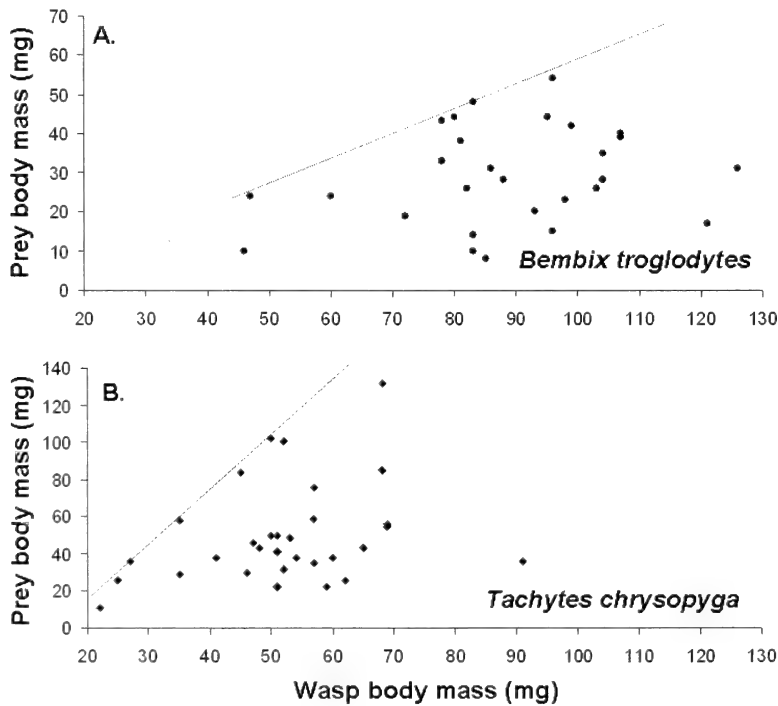


Fig. 2. The effect of wasp size on prey size in two solitary wasps. a. *Bembix troglodytes* from south Texas. b. *Tachytes chrysopyga obscurus* from northern Illinois. The lines were fitted by eye to each graph to demonstrate the maximum prey size for wasps of a given body mass.

marginal FMR of 0.179, which lies within the 95% confidence interval of loaded FMR (0.16 to 0.19).

However, the range of prey mass (11 to 132 mg) resulted in a very broad distribution of FMRs, with many individuals far above (maximum = 0.26) and many far below (minimum = 0.099) the predicted value (Fig. 1B). At times, prey-loaded *T. chrysopyga* were fast, maneuverable and difficult to capture. However, some individuals performed short, hopping flights along the ground and were easily caught. It was very common for the females with prey to land, perhaps even releasing their prey for a few seconds, en route to their burrows. We never observed prey stealing, nor did we ever see conspecific females lurking around the burrows of others. In fact, we found small numbers of abandoned prey in the area of the nest aggregation. Although satellite flies were often observed closely trailing prey-laden *S. speciosus*, perching near and entering their burrows, we never saw evidence of such flies similarly harassing female *T. chrysopyga* in the same area.

During much of the day, many *T. chrysopyga* were flying about low to the ground, though some were certainly males. The burrows were small and relatively inconspicuous, with entranceways sometimes near that of an eastern cicada killer. There was no obvious tumulus near the *T. chrysopyga* entranceway, though the small amount of dirt could easily have been displaced by weather or other disturbances. Entranceways appeared to be open, although they could have been sealed deeper in the burrow.

Prey of *T. chrysopyga* were diverse Orthoptera, including Gryllidae (16 Enoplerinae, 7 Oecanthinae), Tettigoniidae (1 Conocephalinae, 3 Copiphorinae) and Acrididae (8 Cyrtacanthacridinae). The sole adult among the prey was a meadow grasshopper (Conocephalinae).

There was no significant relationship between wasp body mass and prey body

mass in *T. chrysopyga*. But, as in *B. troglodytes*, small wasps were restricted to the smallest prey, while larger wasps carried a greater range of sizes of orthopterans (Fig. 2B).

*B. troglodytes* was significantly larger than *T. chrysopyga* in both body mass ( $P < 0.0001$ ,  $T = -10.85$ ,  $df = 77$ ) and thorax mass ( $P < 0.0001$ ,  $T = -12$ ,  $df = 76$ ). Unladen FMR was significantly higher in *B. troglodytes* ( $P < 0.0001$ ,  $T = -10.25$ ,  $df = 76$ ), as was laden FMR ( $P < 0.0001$ ,  $T = -10.25$ ,  $df = 55$ ). However, prey mass was significantly higher in *T. chrysopyga* than *B. troglodytes* ( $P = 0.0025$ ,  $T = 3.15$ ,  $df = 62$ ).

## DISCUSSION

### *Bembix troglodytes*

At first glance, *B. troglodytes* appears to be a suboptimal forager, at least in the context of our FMR-based model. The wasps could in theory decrease the time spent hunting and the number of hunting trips by simply capturing and carrying larger flies. This strategy would doubtless increase the number of offspring that could be reared during the wasps' short life spans, but there may be mitigating factors involved. Larger flies may be less available or more difficult, energetically expensive and time-consuming to capture. The flies that were captured had lower FMR than unladen *B. troglodytes*. FMR is a useful indicator of maneuverability (see Marden 1989, Marden and Chai 1991). Hence, *B. troglodytes* should have been able to capture the flies on the wing. Prey records for *Bembix* include fast-flying tabanids (Evans 1957).

It is possible that the foraging strategy of *B. troglodytes* minimizes prey stealing. Few wasps returning with prey made it to their burrows unchallenged, and though some of the attacking conspecifics could have been males attempting to mate, theft by females was frequent. Evans (1957) did not report prey stealing in *B. troglodytes*, but the aggregations he studied were relatively

diffuse. Ours was rather dense, which increases the likelihood of thievery or harassment by males. Evans (1957) did report prey stealing in five of ten species of *Bembix* examined. In the related wasp *Stictia heros* (Fabr.), in which prey theft is common, the probability of being attacked is directly related to the size of prey (Villalobos and Shelly 1996). These authors suggest that female *Stictia* carrying large prey were more vulnerable because of their lower flight speed and maneuverability. Therefore, if *B. troglodytes* females took larger flies, they would likely suffer greater rates of conspecific attack. Small prey help them maintain a high level of maneuverability, as we observed, and probably improve the likelihood of successful transport of the prey all the way to the burrow. *Bembix* females can compensate for small prey size by increasing the number of prey.

### *Tachytes chrysopyga*

On first appraisal, *T. chrysopyga* appears to be an optimal forager (using our simple FMR-based model), its loaded FMR being indistinguishable from the predicted value that would maximize load carriage. On average, *T. chrysopyga* takes prey that make full use of its load-lifting capacity. However, upon closer inspection, *T. chrysopyga* is, in fact, highly variable in the size of prey it takes, and consequently, the magnitude of loaded FMR it experiences. These results are comparable to those of Elliot and Salbert (1981), who found that *T. tricinctus* (F.) prey varied from 36.3 to 214 mg, averaging 93.8 mg. These prey are about twice the size of those of *T. chrysopyga*, which is not surprising, as *T. tricinctus* females, averaging 126.5 mg, are over twice the size of *T. chrysopyga*. However, the approximately tenfold range in prey mass in both species may reflect a similarly opportunistic foraging behavior. Prey need not be exceedingly small, as prey stealing is not apparent in these species. Overloading is compensated by behavior – short, hopping flights being adequate to return some

prey to the burrow. Prey need not be exceedingly large either, as *Tachytes* provisions with a variable number of prey (Evans and Kurczewski 1966), and greater numbers could compensate for smaller size.

In spite of being ground-nesting digger wasps with many behaviors in common, *B. troglodytes* and *T. chrysopyga* provide interesting contrasts in foraging strategy. As the vast majority of its prey are flightless, *T. chrysopyga* does not require great maneuverability (bestowed by high unladen FMR) to capture them, as does *B. troglodytes*. *Bembix troglodytes* is a large wasp that takes many, small prey, while *T. chrysopyga* is a small wasp that takes fewer, larger prey (Fig. 2). Both revealed their maximum prey size, as demonstrated by the nearly straight line that can be drawn through the highest points (at a give body size) in Figs 2 A and B. For *B. troglodytes*, the maximum is somewhat below the wasp's own body mass, while for *T. chrysopyga* it is well above the wasp's body mass. In each species of wasp, the same predictions were applied and essentially the same methods used. Neither species conformed to these predictions; however, much was learned about the biology and behavior of each wasp.

### ACKNOWLEDGMENTS

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## Revisionary Studies on the Enigmatic Neotropical Ant Genus *Stegomyrmex* Emery, 1912 (Hymenoptera: Formicidae: Myrmicinae), With the Description of Two New Species

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**Abstract.**—The recent increase in leaf litter ants sampling effort in Neotropical wet forests has revealed new and interesting records of the highly specialized myrmicine ant genus *Stegomyrmex* Emery, previously considered as extremely rare. We present a modified diagnosis for the genus and describe *Stegomyrmex bensoni* n. sp. and *S. olindae* n. sp., based on, respectively, workers, males, and gyne (central-north Brazil) and on a single worker (northern Brazil). *Stegomyrmex vizottoi* Diniz (southeastern Brazil) is redescribed and compared with *S. olindae* n. sp.; these species present significant differences in size, sculpturation, and sting apparatus morphology. The males of *S. vizottoi* are described for the first time. A key for workers and queens and a distribution map for the five known *Stegomyrmex* species are provided.

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*Stegomyrmex* is the sole representative of the peculiar and exclusively Neotropical myrmicine tribe Stegomyrmecini (Bolton 2003). These ants have been considered extremely rare by many authors, perhaps due to their cryptobiotic habits enhanced by peculiar soil-binding pilosity (Hölldobler and Wilson 1986), and by the foraging technique they employ (Diniz and Brandão 1993). However, recent collections employing large-scale sampling (e.g. Agosti et al. 2000) have revealed that they are relatively common inhabitants of the dense leaf litter of Neotropical forests.

Emery (1912) described *Stegomyrmex* with a single species, *S. connectens*, based on a gyne and a male from Peru and Bolivia respectively. Emery included *Stegomyrmex* in the Dacetini based on gyne characters. Wheeler (1922) established a new tribe, Stegomyrmicini (sic), with *Stegomyrmex* as its only member. He separated it from the Dacetini mainly by the shape of mandibles and wing venation. Smith (1946) described the second *Stegomyrmex*

species, *S. manni*, from Barro Colorado Island, Panama, and agreed with Wheeler's placement of the genus in an individual tribe.

Bernard (1951) and Lenko (1965) commented on the morphological resemblance of *Stegomyrmex* to some Attini. However, Brown (1949), Brown and Kempf (1960), and Hölldobler and Wilson (1986) considered stegomyrmecine ants more closely related to Basicerotini than to Attini or Dacetini, mainly by the presence of deep antennal scrobes and the soil-binding pilosity. Dlussky and Fedoseeva (1988) considered *Stegomyrmex* as *incertae sedis* in Myrmicinae, without further discussion. However, in the last proposals of Bolton (1994, 2003, 2006 et al.), *Stegomyrmex* is placed in its own tribe within the Myrmicinae. Bolton (2003) commented that the structure of the promesonotum may suggest a relationship between Stegomyrmecini and Pheidolini, but that there is no undisputed evidence for this yet.

Lenko (1965) found a worker of *S. vizottoi* (identified by him as *S. manni*) in the gizzard of a *Conopophaga lineata* Wied (Aves, Conopophagidae). Hölldobler & Wilson (1986) commented on the presumed role of the soil-binding hairs of basicerotine and stegomyrmecine ants in enhancing their camouflage to predators. Diniz (1990) was the first to revise the taxonomy of Stegomyrmecini, describing the third species of the genus, *Stegomyrmex vizottoi*, based on workers and a gyne from Brazil and Paraguay. In the same work, Diniz commented on the relatively slow movements of stegomyrmecine ants.

Diniz and Brandão (1993) were the first to describe the nesting habits of *Stegomyrmex*, based on observations on colonies of *S. vizottoi* from Mirassol, state of São Paulo, Brazil, describing nest architecture, population distribution among nest chambers, different worker behaviors at each part of the nest, and the foraging habits of the workers, which exploit the environment surrounding their nests singly, searching for myriapod eggs.

Recent surveys of leaf litter ants in the Brazilian Atlantic forest and in sparse localities of central and northern Brazil revealed several *Stegomyrmex* specimens, including a remarkable new species described here, and extending considerably the known distribution range of *S. vizottoi*. Our analysis of *S. vizottoi* along its distribution shows, however, that, as presently accepted, it includes two distinct species, recognizable by the surface sculpture, by morphometry, and by differences in the sting apparatus, as we fully describe and comment on below.

In this paper we offer taxonomic notes on the peculiar ant genus *Stegomyrmex*, based on the study of the specimens deposited in the Museu de Zoologia da Universidade de São Paulo ant collection, literature information, and enriched by unpublished observations. We also describe two new species and comment on new records and information regarding these seldom collected ants.

## METHODS

This study was based on the available specimens in the collection of the Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil, which is believed to hold most of the known *Stegomyrmex* specimens. Depository collections are referred to by the following acronyms:

**BMNH** – The Natural History Museum, London, UK.

**CASC** – California Academy of Sciences, San Francisco, California, USA.

**CPDC** – Centro de Pesquisas do Cacau, Itabuna, Bahia, Brazil.

**JLMD** – Laboratório de Zoologia, Campus Jataí, Universidade Federal de Goiás, Brazil.

**LACM** – Los Angeles County Museum of Natural History, Los Angeles, California, USA.

**MCSN** – Museo Civico di Storia Naturale “Giacomo Doria”, Genoa, Italy.

**MPEG** – Museu Paraense Emílio Goeldi, Belém, Pará, Brazil.

**MZSP** – Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.

**USNM** – National Museum of Natural History – Smithsonian Institution, Washington, DC, USA.

The terms for external morphology and surface sculpturing follow, respectively, Bolton (1994, 2000) and Harris (1979). The terms for wing venation follow Brown and Nutting (1950). The reproductive females are here called “gynes”, as suggested by De Andrade and Baroni Urbani (1999).

Measurements were obtained with a micrometric reticule and using the scale of a scanning electron microscope (SEM). All measurements are given in mm, and the abbreviations used are:

**HW**: head width; the maximum width of the head capsule, measured in full face view, at a median transverse line that touches the superior margins of the compound eyes.

**HL**: head length; the maximum measurable length of head capsule excluding the

mandible, measured in full face view, in a straight line from the midpoint of the anterior clypeal margin to the midpoint of the vertexal margin.

**SL:** antennal scape length; the chord length of the antennal scape, excluding the basal condyle and its peduncle.

**WL:** mesosoma length (Weber's length); the diagonal length of mesosoma in profile, from the midpoint of the anterior pronotal declivity to the posterior basal angle of the metapleuron.

**PL:** petiole length; the longitudinal axis of petiole in lateral view.

**PPL:** postpetiole length; the longitudinal axis of postpetiole in lateral view.

**GL:** gaster length; the maximum length of gaster in lateral view, excluding sting.

**TL:** total length; the summed length of HL (plus the closed mandibles), WL, PL, PPL, and GL.

**CI:** cephalic index.  $HW \times 100 / HL$ .

**SI:** scape index.  $SL \times 100 / HW$ .

The SEM images of *Stegomyrmex* specimens were obtained from a single specimen of each species. The specimens were previously cleaned in acetone, critical-point dried in a Balzer (Bal-Tec® CPD 030), and sputtered over with gold (Bal-Tec® SCD 050). After that, the specimens were mounted on the tip of metallic triangles using silver glue and then affixed to stubs for the electron microscopy. The images were obtained under several magnifications (40 to 300x), according to the size of the specimen and/or structure observed. Finally, the images were edited (Adobe PhotoShop 7.0®) to enhance some brightness and contrast details.

We studied also the sting apparatus of the species from which we had enough individuals. The sting was obtained by rehydrating ants in 70% ethanol, extracting the terminal segments from the gaster, clearing them in 55–60°C lactophenol for five minutes (or longer if necessary), rinsing twice in 70% ethanol, and twice in 95% ethanol. After the clearing process, the sting apparatus was dismembered, soaked

in xylene, and then mounted in Canada balsam for observation and illustration under optical microscope. The terms for sting apparatus morphology follow Kugler (1978).

Coordinates of localities were obtained from the information on the specimens labels and after consulting the ENCARTA World Atlas® (Microsoft); they were plotted on the distribution map generated by the software ArcView 3.2 GIS®.

When citing label data, we present additional information between brackets, explanation of codes on the labels, eventual corrections to the misprints, and reference to the notebooks from which we took information regarding the localities and/or the biology of the species.

## RESULTS

### *Stegomyrmex* Emery, 1912

*Stegomyrmex* Emery, 1912: 99. Gyne. Type species: *Stegomyrmex connectens*, by monotypy. Emery, 1912: 101 (placement in Dacetini); Emery, 1914: 42 (placement in Dacetini); Forel, 1917: 246 (placement in Dacetini); Emery, 1924: 314 (placement in Dacetini, diagnosis, catalogue); Wheeler, 1922: 668 (establishment of Stegomyrmecini [as Stegomyrmicini]); Donisthorpe, 1943: 727 (placement in Dacetini, list of type specimens); Smith, 1946: 286 (revision); Brown and Kempf, 1960: 162 (systematic notes); Lenko, 1965: 201 (distribution and biology); Kempf, 1972: 242 (catalogue); Wheeler and Wheeler, 1985: 258 (tribal classification); Hölldobler and Wilson, 1986: 16 (pilosity); Dlussky & Fedoseeva, 1988: 81 (*incertae sedis* in Myrmicinae); Diniz, 1990: 277 (revision, species key); Hölldobler and Wilson, 1990: 15 (tribal classification); Brandão, 1991: 379 (catalogue); Diniz and Brandão, 1993: 301 (biology); Bolton, 1994: 106 (catalogue); Bolton, 1995a: 1052 (census); Bolton, 1995b: 392 (catalogue); Serna, 2002: 217 (first record for Colombia); Bolton, 2003: 255 (diagnosis, synoptic classification); Fernández and Ospina, 2003: 49 (census); Fernández, 2003: 325 (genera list for Neotropics); Bolton et al., 2006 (catalogue).

**Worker.** Monomorphic. 5 to 6.5 mm in length. Reddish brown to black. Integument thick, shining and in general densely areolate, except for *S. bensoni*. Pilosity conspicuous and bizarre; hairs varying from short, subdecumbent and filiform to long, suberect, and variably branched; mandibles sparsely covered by long filiform hairs; anterior margin of clypeus bearing one or two pairs of very long setae, reaching half the length of mandibles, but without an isolated median seta; appendages covered by short decumbent hairs and by a fine and dense appressed pubescence; inferior corners of pronotum with a dense row of plumose hairs.

Head subtrapezoidal with vertexal margin slightly depressed to slightly convex; occipital corners angulate; broader posterad. Palpal formula 2:2. Labrum bilobed. Mandible triangular, long, strongly curved down apically and with the blades crossing apically when mandibles are closed; masticatory border multidenticulate (total dental count 12–15), with the apical tooth longer than the preceding ones. Median portion of clypeus narrow, flat and vertical, not bicarinate, quite narrowly inserted between the frontal lobes. Frontal lobes enormously expanded anterolaterally and projected far out over the lateral portions of clypeus and mandibles. Each frontal lobe covering dorsally a very deep antennal scrobe; in full face view, space between frontal lobes narrowest near the middle of head, revealing the compound eyes; clypeus and basal portion of mandible entirely concealed by the frontal lobes. Frontal area impressed, glabrous and smooth, the anterior suture obsolete. A shallow groove, almost devoid of any sculpture, present on each side of the head dorsum, extending from the frontal area to the occipital corner of head, the two grooves meeting anteriorly, forming a noticeable V. Antenna with 12 segments, with a three-segmented club; antenaral scape slender, curved basally and broader at apex. Compound eye exceedingly small, oval in shape, almost indistinct

from the integument sculpture; placed on the sides of head immediately beneath the antennal scrobe, but visible when head is in full face view.

Mesosoma, in dorsal view, slender, widest at the level of the anterior area of pronotum. Promesonotum evenly rounded in profile, dome-like; anterosuperior corner of anepisternum set much lower than the adjacent surface, forming a deep fovea; promesonotal suture almost obsolete in some individuals. Mesonotum elongate with posterior portion sloping down; metapropodeal impression relatively broad and usually shallow, except for *S. bensoni*. Propodeum, in side view, variably convex dorsally, and with the declivity sinuous; propodeal spiracles low on side and raised in prominent, subcylindrical protuberances; propodeal spines short and more or less acute; propodeal lobes large and usually projected over the petiolar peduncle. Legs relatively long; femora and tibiae moderately incrassated; tarsal claws simple; metatibial spurs absent.

Petiole long and pedunculate, with about twice the length of the postpetiole; petiolar node variably convex in profile; ventral carina present and bearing 0–2 blunt anterior projections. Postpetiole approximately as long as broad, globose, without ventral process. Gaster oval, without basal shoulder; tergite of abdominal segment IV (first gastral) not broadly overlapping sternite on gaster ventral surface.

Sting apparatus. Spiracular plate with spiracle placed ventrally; anal plate with several sensillae; lancet with a pair of functional valves; furcula with indistinct dorsal arms.

**Gyne.** Like conspecific worker, with the modifications expected for myrmicine gynes. Anterior ocellus slightly larger than posterior ones. Notauli and parapsidal lines usually indistinct from surrounding sculpture; prescutellum with central area indistinct, scutoscutellar sulcus shallowly impressed, with transversal rugulae varying in number and forming distinct cells;

lateral wing of prescutellum not projecting laterally; scutellum semicircular, with its posterior half always sloping down and with posterior border concave; propodeal spines shorter than in conspecific workers.

Forewing with distinct and strongly colored stigma; longitudinal veins Sc+R, SR, M+Cu, and A present. Cells R, Cu and 1M closed. Hind wing with Sc+R extending shortly beyond point where they connect to M, which extends as a tubular vein up to the wing distal border; Cu cell closed and very short; six to eight submedian hamuli.

**Male.** Dark brown to black, with appendages and gaster usually lighter. Integument densely sculptured, opaque or nearly so, except for the postpetiole and gaster which are smooth and shining; appendages very finely punctate. Pilosity composed of fine hairs, whitish to golden, mostly curved or suberect on body, sparser on metasoma. Apressed pubescence on antennae and legs.

Head broadest across compound eyes, narrowed anteriorly; median portion of vertexal margin usually weakly convex; occipital corners rounded; ocelli prominent. Mandible relatively developed and subtriangular; masticatory border multidenticulate, with the apical tooth much more developed than the others. Clypeus broad. Frontal lobes not so developed as in the conspecific gynes and workers, but concealing the antennal insertions, forming a short and shallow antennal scrobe. Antennae long and slender with 13 segments; scapes relatively short.

Mesosoma robust; prescutellum separated from scutellum by an impression with short longitudinal rugae. Scutellum narrow posterad. Metanotum narrow, with blunt median tumosity. Propodeum dorsal face flat, steeply sloping posterad, unarmed. Legs slender, middle and hind tibiae without apical spurs; tarsal claws slender and simple. Wing venation as in the gynes.

Petiole clavate, pedunculate, and with a long, low, rounded node. Postpetiole as broad as long, attached to the gaster by almost its full width. Gaster elongate, with first segment occupying most of its length; visible apical segments subequal in length.

*Comments.*—We revise the *Stegomyrmex* diagnosis presented by Diniz (1990) in order to include information on the shape of the head and on the structure of the alate's mesosoma, besides features present in *S. bensoni* **n. sp** and *S. olindae* **n. sp**. Apomorphies for *Stegomyrmecini* defined by Bolton (2003) hold true for the new species.

Despite the recent information regarding these seldom collected ants, the phylogenetic position of *Stegomyrmex* remains truly enigmatic. The affinities with Dacetini and Attini, proposed in the past, seem improbable by the significant differences in habits and morphology. Despite the body sculpturation patterns and the presence of specialized pilosity approximating *Stegomyrmex* and *Basicerotini* (Hölldobler and Wilson 1986), the possibility of homoplasy can not be presently discarded.

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#### REVISED KEY TO THE *STEGOMYRMEX* SPECIES (WORKERS AND GYNES)

1. Integument of mesosoma predominantly smooth and shining; body covered mainly by sparse aggregations of somewhat curved and multibranching hairs; metapropodeal groove deeply impressed; petiole without anteroventral spines (state of Pará, Brazil) ..... *S. bensoni* **sp. n.**
- Integument of mesosoma predominantly sculptured, areolate; body covered mainly by sparse and erect clavate setae; metapropodeal groove only moderately impressed; petiole with at least one anteroventral spine ..... 2

2. Petiole with two anteroventral spines; inferior margin of pronotum with a row of filiform hairs; known only from the gyne (Peru and Bolivia) . . . *S. connectens* Emery
- Petiole with a single anteroventral spine; inferior margin of pronotum with a row of plumose hairs . . . . . 3
3. Promesonotum much higher than propodeum, in lateral view; propodeal spines blunt and directed posteriorly; in dorsal view propodeal spiracles strongly projected laterally (Costa Rica, Panama and Colombia) . . . . . *S. manni* Smith
- Promesonotum slightly higher than propodeum, in lateral view; propodeal spines subtriangular, acute and directed upwards; in dorsal view propodeal spiracles not strongly projected laterally . . . . . 4
4. Mesosoma length  $\geq 1.59$  mm; mesosoma partially sculptured, with foveae sparsely set on the polished integument; metapropodeal impression without a projecting tubercle; nuchal area predominantly smooth; in dorsal view basal face of propodeum relatively narrow (northern Argentina, Paraguay and southeastern Brazil) . . . . . *S. vizottoi* Diniz
- Mesosoma length  $< 1.59$  mm; mesosoma strongly sculptured, with the integument completely areolate; metapropodeal impression with a projecting tubercle; nuchal area predominantly sculptured; in dorsal view basal face of propodeum relatively broad (central-north Brazil) . . . . . *S. olindae* sp. n.

*Stegomyrmex bensoni* n. sp.  
(Figs 1, 7)

*Holotype worker*.—**BRAZIL**: Pará, Canaã dos Carajás (06°44'49"S, 50°21'05"W) (Gruta NV06) 22–28.ii.2005 (Andrade & Arnoni) [MZSP].

*Worker description*.—HW 1.26; HL 1.09; ML 0.61; SL 0.84; WL 1.77; PL 0.78; PPL 0.45; GL 1.70; TL 6.40; CI 115.56; SI 66.35. Color reddish brown. Basal portion of mandible finely and densely striate, with large and sparse piligerous punctures, apical portion and masticatory border mostly smooth and shining; inner surface of antennal scrobes with fine, dense, transversal and concentric striation; dorsal surface of head predominantly smooth and shining, with scattered punctures near the vertexal border; margin of frontal lobes finely areolate-rugose; central portion of each frontal lobe virtually translucent, so that is possible to observe the inner surface of the antennal scrobes near the insertions of antennae; antennae opaque and finely punctate; lateral and ventral surface of head deeply areolate; occipital face of head smooth and shining except for the nuchal collar which is regularly and deeply scrobiculate; mesosoma almost entirely smooth

and shining, except for a few scattered punctures at the inferior portion of meso and metapleuron; legs smooth and rather opaque; petiole and postpetiole smooth and shining with some sparse piligerous punctures; dorsum of gaster feebly shining and with sparse and fine punctuation.

Pilosity golden and extremely diverse; sparse filiform hairs covering the dorsum of mandible, external borders of frontal carinae, antennal scapes, legs, dorsum of mesosoma and metasoma; long, slightly curved, moderately clavate hairs present on dorsum of head and promesonotum; short, curved, branched hairs present on head occipital corners, dorsal surface of legs and gaster; posteroventral corners of head, anterior and lateral portions of promesonotum, dorsum of metanotum and propodeum, ventral and lateral faces of waist and anterior portion of gaster (in special the sternite) with aggregations of long, multibranched (plumose), curved hairs, so that the integument is hardly visible in these areas.

Head vertexal margin convex in the middle. Compound eyes exceedingly small, with circa three almost indistinct facets at the maximum diameter.

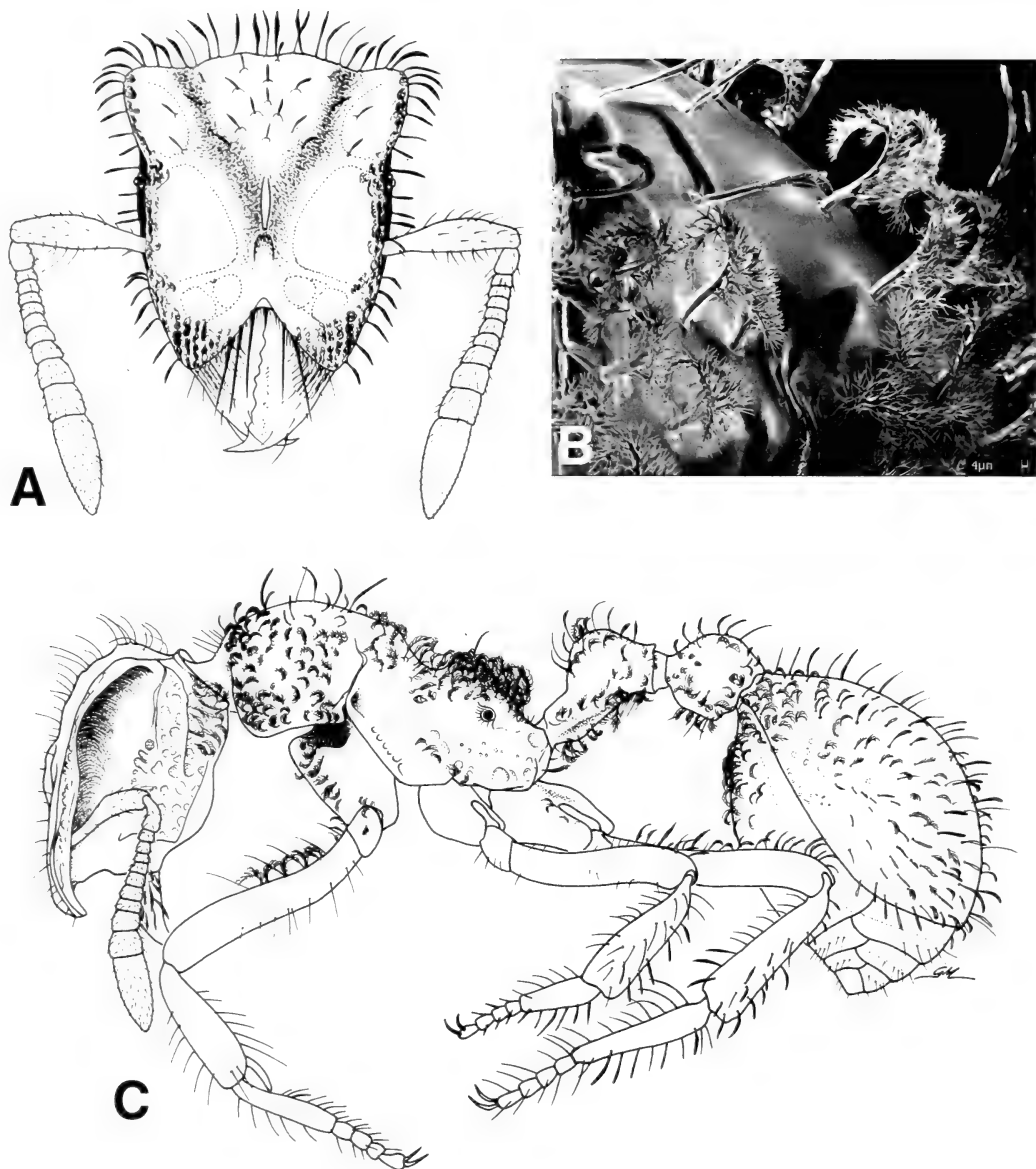


Fig. 1. *Stegomyrmex bensoni* n. sp., worker. A, head in full face view; B, SEM close-up view of promesonotal multibranch hairs; C, habitus.

Promesonotum strongly convex dorsally; metapropodeal groove deeply impressed; propodeal spines short and subtriangular, entirely covered by the propodeum pilosity; propodeal spiracle wide open, and moderately projected laterad; propodeal lobes subquadrate and weakly projected over the petiolar peduncle.

Petiole elongate, slightly arched, with a prominent rounded node; ventral carina of

petiolar peduncle without anterior projections. Postpetiole strongly convex dorsally and without ventral processes. Gaster oval and robust.

*Gyne*.—Unknown.

*Male*.—Unknown.

*Etymology*.—Species named after the prominent Brazilian-American ecologist, Woodruff Whitman Benson, well known for the study of ecological interactions in



Brazilian ecosystems. He organized for several years a field course on Ecology (graduate program of the Universidade Estadual de Campinas, São Paulo), given for several years in the Serra dos Carajás, Pará, where generations of Brazilian graduate students had their first field experience, and where the unique known specimen of *S. bensoni* was found.

*Comments.*—The peculiar multibranched pilosity, allied to the deep metapropodeal groove, and the absence of anteroventral petiolar projections, easily separate this species from all others in the genus.

The single worker known thus far was captured by our colleague arachnologist, Renata Andrade, while searching for cavernicolous pseudoscorpions in Serra dos Carajás, southeastern state of Pará (Amazon region), Brazil. The finding represents the first record of a stegomyrmecine ant in the Amazon Region.

Despite the fact that the only known specimen was collected inside a cave, near its mouth, there is no undisputed evidence that *Stegomyrmex bensoni* is restricted to this habitat.

### *Stegomyrmex olindae* sp. n.

(Figs 2, 3, 6, 7)

*Holotype worker.*—**BRAZIL:** Tocantins, Palmeiras do Tocantins (06°40'12"S, 47°31'48"W) (Winkler n.3) 14–19.i.2005 (Silva, R.R. and Silvestre, R.) [MZSP].

*Stegomyrmex vizottoi* Diniz, 1990: 290 (in part).

*Paratypes.*—**BRAZIL:** Bahia: Ilhéus, CEPEC-área Zoológ. (Km22 Ilhéus-Itabuna) x.1986 (J. Delabie) (1 worker) [MZSP]; Porto Seguro, E.E. Pau Brasil (16°23'33"S, 39°10'99"W) (Winkler n.1) 16.vi.2000 (Santos, J.R.M and Soares, J.C) (1 worker) [MZSP]; **Maranhão:** Açailândia, Horto Faz. Pompéia (04°52'30"S, 47°17'40"W) 13–22.ii.2006 (Silva, R.R. and Feitosa, R.M.) (1 worker) [MZSP]; Estreito, Fazenda Itaueiras (06°31'54"S, 47°72'16"W) 07–13.i.2005 (Silva, R.R. and Silvestre, R.) (2 workers and 1 gyne) [MZSP]; same data (1 worker) [BMNH]; same data (1 worker) [CDPC]; same data (1 worker

and 1 gyne) [LACM]; **Mato Grosso:** Sto. Antônio de Leverger, Águas Quentes (High Cerrado) (n. 0184) 26.x.1984 (J.C. Trager) (1 worker) [MZSP]; **Minas Gerais:** Timóteo, P.E. do Rio Doce (TM3–8) 07.v.2005 (Esteves, F.A.) (1 worker) [MZSP]; **Tocantins:** Palmeirante (Mata Ciliar/Cerradão) (07°52'25"S, 47°31'48"W) 10–15.xii.2001 (Albuquerque and Silva) (1 worker) [MZSP]; same data (1 worker) [CASC]; Araguaçema (08°59'20"S, 49°40'41"W) 16–30.xi.2005 (Silva, R.R. and Feitosa, R.M.) (1 worker) [MZSP]; same data (1 worker) [MPEG]; same data (1 worker) [USNM].

*Worker description.*—Holotype (workers N= 8); HW 1.09 (1.04–1.22); HL 0.97 (0.92–1.07); ML 0.49 (0.46–0.49); SL 0.74 (0.69–0.80); WL 1.43 (1.33–1.53); PL 0.68 (0.61–0.70); PPL 0.39 (0.33–0.44); GL 1.36 (1.24–1.50); TL 5.32 (5.01–5.70); CI 113.75 (104.88–114.63); SI 66.59 (63.83–67.44). Dark brown to ferruginous, with appendages somewhat lighter. Mandible finely and densely striate, with large and sparse piligerous punctures, except for the masticatory border and dorsum of apical portion which are smooth and shining; inner surface of antennal scrobes punctate and with fine transversal striation; central disc of head and external margin of frontal lobes densely areolate-rugose; oblique lateral grooves of head, frontal area and posterior portion of frontal lobes with smooth areas and sparse punctuation; anterior portion of frontal lobes shallowly areolate and with irregular longitudinal rugulae; antennae opaque and finely punctate; lateral, ventral and occipital surfaces of head deeply areolate; mesosoma (including the anterior coxae), petiole, and postpetiole entirely and deeply areolate; legs opaque and weakly sculptured; surface of gaster deeply and densely foveolate.

Pilosity cream-colored. Body covered by abundant, long, slightly stiffened, moderately clavate hairs, somewhat shorter in the external borders of frontal lobes, antennal scapes, and legs; mandible with long, sparse filiform setae; short, curved, plumose hairs present on the posteroventral corners of head, inferior and lateral por-

tions of pronotum, and more rarely on the lateral surfaces of waist; occipital face of head and lateral surface of mesonotum, metanotum, and propodeum virtually glabrous.

Vertexal border gently convex and with a discrete concavity medially. Compound eyes with circa six facets at maximum diameter.

Promesonotum strongly convex dorsally, in lateral view; promesonotal suture distinct only in the lateral faces of promesonotum; anepisternum set lower than the adjacent surface; metapropodeal groove relatively large, moderately impressed and with a median triangular projection; propodeal spines subtriangular, directed upwards and with the posterior faces enlarged medially; propodeal spiracles relatively wide, and considerably projected posterad; propodeal lobes rounded and moderately projected over the petiolar peduncle. In dorsal view, the propodeum is relatively broad, slightly narrower than the promesonotum.

Petiole elongate, gently arched, with a relatively long rounded node; ventral carina of peduncle with a well-developed anterior projection. Postpetiole with a long and moderately convex dorsal face, without ventral projections. Gaster oval and robust.

Sting apparatus (Fig. 3): Spiracular plate subquadrate, not extending towards the medial connection; margin of medial connection sclerotized; dorsal notch absent; spiracle relatively wide and set close to the posterior margin of plate; anterior apodema narrow with the medial region with a distinct angle; ventral edge vestigial, marked only by a weak projection. Quadrate plate with the dorsal region as broad as the ventral region, except for the apodema; apodema area smaller than the plate body; dorsal margin convex; apex of anterodorsal corner rounded; posterior margin complete. Anal plate with the arc rounded and strongly sclerotized; apical margin rounded and weakly definite; anal

sensilla sparsely distributed over the plate dorsum. Oblong plate with long posterior apodema; subterminal tubercle with rounded apex; postincision well developed. Gonostylus one-segmented and with six chaetae, five subequal in length and one extremely long; terminal sector short and membranous, with dorsoterminal and companion chaetae present. Triangular plate as long as broad, without tubercles or projections. Lancets with functional valves; sensorial barbles absent; dorsal and ventral margins converging towards the apex. Sting shaft weakly sclerotized, probably not perforating; dorsum of valve chamber indistinct in profile; internal apophysis absent; basal connection gently concave; anterolateral processes well developed, as broad as the furcula lateral arms; campaniform sensilla absent. Dorsal arm of furcula relatively reduced, indistinct; lateral arms well developed; fulcral articulation connected to the sting basis only by its lateral corners.

*Gyne*.—(N= 2); HW 1.24–1.26; HL 1.04; ML 0.52–0.53; SL 0.78; WL 1.82; PL 0.80–0.83; PPL 0.46–0.49; GL 1.82–1.84; TL 6.50–6.51; CI 118.60–120.93; SI 62.12–62.75. Like conspecific worker, with the modifications expected for myrmicine gynes. Plumose hairs restricted to the posteroventral corner of head and inferior corner of pronotum. Compound eyes with circa 11 facets at maximum diameter; propodeal spines drastically reduced; posterior face of propodeum vertical in side view, reaching the propodeal lobes in a rounded angle. Wings unknown.

*Male*.—Unknown.

*Etymology*.—This species is named after Florinda Gonzaga Teixeira, a long-term and always large-hearted steward of the MZSP ant lab, at the occasion of her retirement. She prefers to be called “Dona Olinda”, hence the specific name.

*Comments*.—While examining specimens of *Stegomyrmex vizottoi* from the MZSP collection, one of us (RMF) noticed that

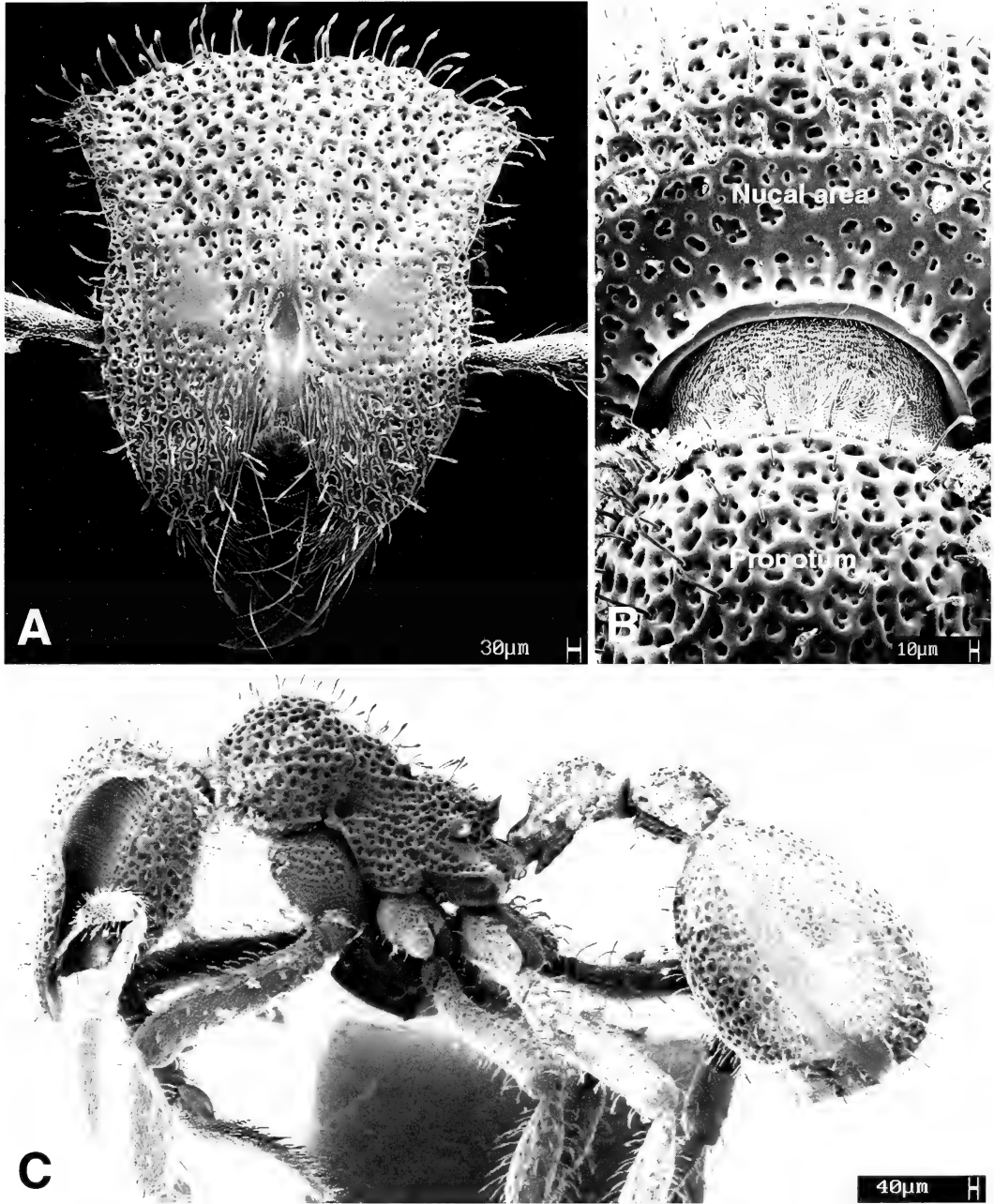


Fig. 2. *Stegomyrmex olindae* n. sp., worker (SEM). A, head in full face view; B, close-up view of nuchal area; C, habitus.

there was a morphologically distinct sub-group of individuals, all collected in the northern range of *S. vizottoi* distribution. Diniz (1990) already mentioned, while commenting on the original description of *S. vizottoi*, that a specimen from Ilhéus, state

of Bahia (northeastern Brazil) presented the lateral faces of the mesosoma more densely sculptured and the basal face of propodeum relatively enlarged in dorsal view in relation to other specimens, but he considered these characteristics as geographical variations

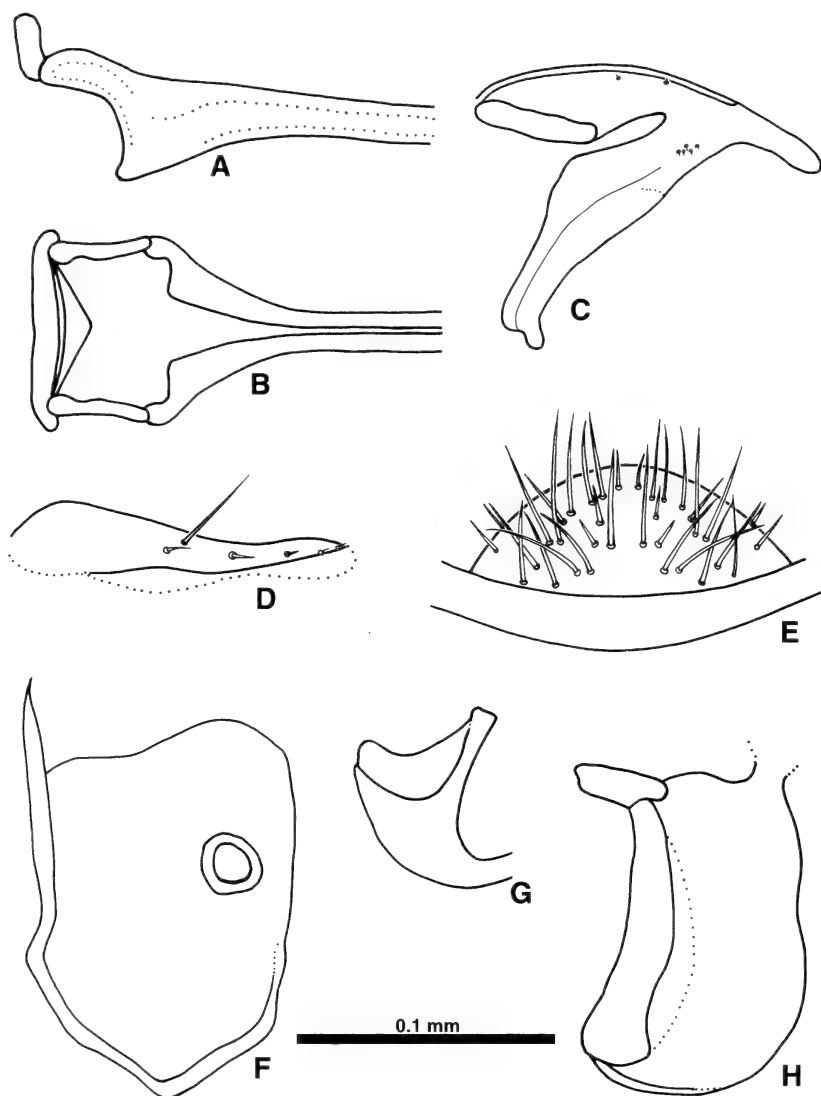


Fig. 3. *Stegomyrmex olindae* n. sp., worker sting apparatus. A, sting and furcula in profile; B, sting and furcula in dorsal view; C, oblong plate; D, gonostylus; E, anal plate; F, spiracular plate; G, triangular plate; H, quadrate plate.

and considered this specimen to belong to *S. vizottoi*. The study of the recently collected stegomyrmecine specimens deposited in the MZSP collection, led us to recognize this specimen and several others as a different and undescribed species.

This species can be separated from the related *S. vizottoi* by: the smaller size (Fig. 6), the nuchal area and the whole mesosoma densely areolate-rugose, the metapropodeal groove bearing a median

tumosity, and by the differences in the sting apparatus morphology.

*Stegomyrmex olindae* has been recorded in sparse localities in the Brazilian states of Bahia, Maranhão, Minas Gerais, Mato Grosso, and Tocantins (central-north Brazil). The specimens are usually collected in the leaf litter of mature wet forests. Nothing is known about its natural history.

The MZSP collection received recently two stegomyrmecine males from Itabirito,

state of Minas Gerais, Brazil. Despite the fact that these ants have been collected within the range of *S. olindae*, they are very similar to the males of *S. vizottoi*, differing only in discrete details of wing venation. So, we decided not to include these males in the present study until we have additional material from Minas Gerais.

***Stegomyrmex vizottoi* Diniz 1990**

(Figs 4, 5, 6, 7)

*Stegomyrmex vizottoi* Diniz, 1990: 290. **Holotype worker.** BRAZIL: São Paulo, Mirassol x.1971 (J.L.M. Diniz) (JLMD code 361) (MZSP code 11.029) [MZSP] (examined). Diniz and Brandão, 1993: 301 (biology).

*Stegomyrmex manni* Smith, 1946: 288 (in part). Lenko, 1965: 201 (distribution and biology); Kempf, 1972: 242 (catalogue).

**Worker description.**—Holotype (workers N= 7); HW 1.26 (1.17–1.33); HL 1.07 (1.00–1.14); ML 0.58 (0.51–0.61); SL 0.80 (0.76–0.85); WL 1.65 (1.59–1.77); PL 0.78 (0.70–0.80); PPL 0.46 (0.41–0.49); GL 1.60 (1.48–1.70); TL 6.14 (5.72–6.48); CI 118.18 (116.67–118.60); SI 63.46 (61.82–67.96). Dark brown to black, with ferruginous appendages. Mandible finely and densely striate, with large and sparse piligerous punctures, except for the masticatory border and dorsum of apical portion which are smooth and shining; inner surface of antennal scrobes feebly striate and with punctation restricted to the region of antennal insertions; central disc of head and external margin of frontal lobes moderately areolate; oblique lateral grooves of head, frontal area and posterior portion of frontal lobes predominantly smooth and shining, with a few sparse punctures; anterior portion of frontal lobes weakly areolate and with irregular longitudinal rugulae; antennae opaque and finely punctate; lateral and ventral surfaces of head deeply areolate; occipital face of head mostly smooth and shining, except for the nuchal collar which is uniformly scrobiculate; mesosoma partially foveolate, with the dorsum densely

sculptured and the lateral surfaces mostly smooth and shining with a few sparse foveae; anterior coxae, petiole, and postpetiole entirely and deeply areolate-rugose; legs opaque and weakly sculptured; surface of gaster finely and deeply foveolate.

Pilosity cream-colored. Body covered by slightly stiffened, moderately clavate hairs, somewhat shorter in the external borders of frontal lobes, antennal scapes, and legs; mandibles with long, sparse filiform setae; posterior portion of ventral surface of head and anteroinferior portion of pronotum with short, curved, plumose hairs; occipital face of head and lateral surface of mesonotum, metanotum, and propodeum glabrous.

Head relatively broad in frontal view. Vertex margin slightly convex and with a discrete concavity medially; eyes with circa six facets at maximum diameter.

Promesonotum relatively elongate in dorsal view, strongly convex dorsally in lateral view; promesonotal suture distinct only in the lateral faces of promesonotum; anepisternum set lower than the adjacent surface; metapropodeal groove large, shallowly impressed and without median projections; propodeal spines relatively short, subtriangular, with the apexes directed upwards and with the posterior faces straight; propodeal spiracles weakly projected posterad; propodeal lobes rounded and projected over the petiolar peduncle. In dorsal view, propodeum as narrow as the promesonotum.

Petiole elongate, slightly arched, with a long rounded node; ventral carina of peduncle with a well-developed anterior projection. Postpetiole globose, with the dorsal face gently convex, without ventral projections. Gaster oval and robust.

Sting apparatus (Fig. 5): Spiracular plate subquadrate, not extending towards the medial connection; margin of medial connection sclerotized; dorsal notch present; spiracle moderately wide and placed close to the posteroventral region of plate; anterior apodema enlarged medially and with an apical tubercle; ventral edge well

developed. Quadrate plate with the dorsal region broader than the ventral region, excluding the apodema; apodema area smaller than the plate body; dorsal margin flattened and sloped; anterodorsal corner of apex acute; posterior margin divided. Anal plate with the arc strongly sclerotized; apical margin triangular and well definite; anal sensillae equally developed and restricted to the posterior border of plate. Oblong plate with short posterior apodema; subterminal tubercle acute apically; postincision well developed. Gonostylus one-segmented and with five chaetae subequal in length; terminal sector short and membranous, with dorsoterminal and companion chaetae present. Triangular plate as long as broad; only the median tubercle is present. Lancets with functional valves; sensorial barbles absent; distal portion weakly sclerotized, probably not perforating; dorsal and ventral margins converging towards the apex; outer dorsal wall absent. Sting shaft weakly sclerotized, not perforating; dorsum of valve chamber indistinct in profile; internal apophysis long and well sclerotized, extending along the dorsum of valve chamber; basal connection strongly concave; anterolateral processes well developed, narrowed medially, and as broad as the furcula lateral arms; campaniform sensilla absent. Dorsal arm of furcula indistinct; lateral arms well developed; fulcral articulation connected to the sting basis only by its lateral corners.

*Gyne*.—(N= 1); HW 1.46; HL 1.19; ML 0.65; SL 0.95; WL 2.00; PL 0.92; PPL 0.56; GL 1.99; TL 7.31; CI 122.45; SI 65.00. Like conspecific worker, with the modifications expected for myrmicine gynes. Plumose hairs restricted to the posteroventral corner of head and inferior corner of pronotum. Compound eyes with circa 13 facets at maximum diameter; propodeal spines reduced; posterior face of propodeum slightly inclined in side view, reaching the propodeal lobes in rounded angles. Forewing with strongly colored stigma; longitudinal vein Sc+R nebulous when reaching the stigma;

SR extending distally beyond the stigma as a tubular vein for most of its length; M and Cu also extending distally, initially as tubular veins and then as spectral veins almost reaching the distal wing border; anal vein not extending beyond CU cell. Hind wing with Sc+R extending shortly beyond the point where they connect to M, which extends as a spectral vein to the wing distal border; basally M+Cu does not continue as a tubular vein beyond the junction with 1M; anal vein drastically reduced; seven submedian hamuli.

*Male*.—(N= 4); HW 0.92–0.98; HL 0.80–0.85; ML 0.21–0.24; SL 0.29–0.30; WL 1.89–2.04; PL 0.90–0.95; PPL 0.41–0.49; GL 1.82–1.89; TL 6.07–6.41; CI 114.29–115.15; SI 30.00–31.58. Slightly smaller and slenderer than conspecific gynes. Color black with appendages and gaster somewhat lighter. Integument opaque and densely areolate-rugose, except for the postpetiole and gaster, which are smooth and shining; appendages very finely punctate. Dorsum of head and mesosoma densely covered by whitish, fine, suberect hairs, sparser over the dorsum of the metasoma; appendages with short, subdecumbent hairs.

Head broadest across large bulging compound eyes (situated at the head midlength) rather suddenly narrowed in front of eyes and tapering moderately anterad; median portion of vertexal margin weakly convex; occipital corners rounded; ocelli prominent. Mandible relatively developed, subtriangular, with slightly curved outer borders, rapidly converging in apical half; gently down curved; masticatory border bearing circa seven serial teeth, with the apical tooth much more developed than the others. Clypeus broad and truncate in front. Frontal lobes not so developed as in the conspecific gynes and workers, but concealing the antennal insertions. Frontal carinae short and not expanded laterally, forming a short and shallow antennal scrobe. Antennae long and slender with 13 segments; scape very short, only about twice as long as broad.

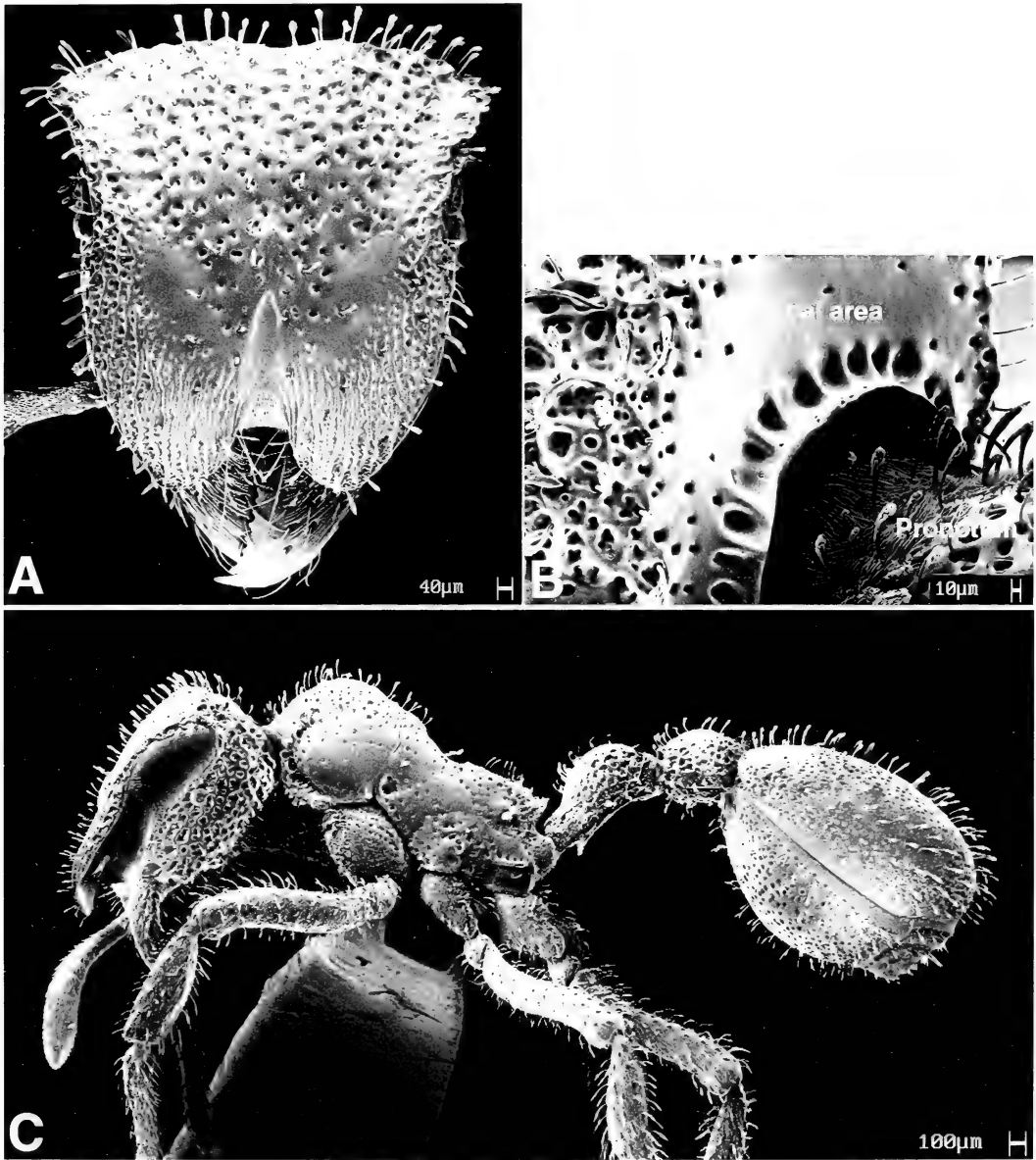


Fig. 4. *Stegomyrmex vizottoi* Diniz, worker (SEM). A, head in full face view; B, close-up view of nuchal area; C, habitus.

Prescutum with more or less distinct anteromedian carina; notauli shallow and complete, with transversal costulae. Parapsidial furrows as fine shining lines; parapsides more or less impressed behind, but each with a sharp, raised posterolateral margin. Prescutellum separated from scutellum by an impression bearing short

longitudinal rugae. Scutellum narrow posterad. Metanotum narrow, with blunt median tumosity. Propodeum with dorsal face flat, steeply sloping posterad, and unarmed. Legs slender, middle and hind tibiae without apical spurs; tarsal claws slender and simple. Wings brownish, with opalescent bluish reflections; venation as in the gynes.

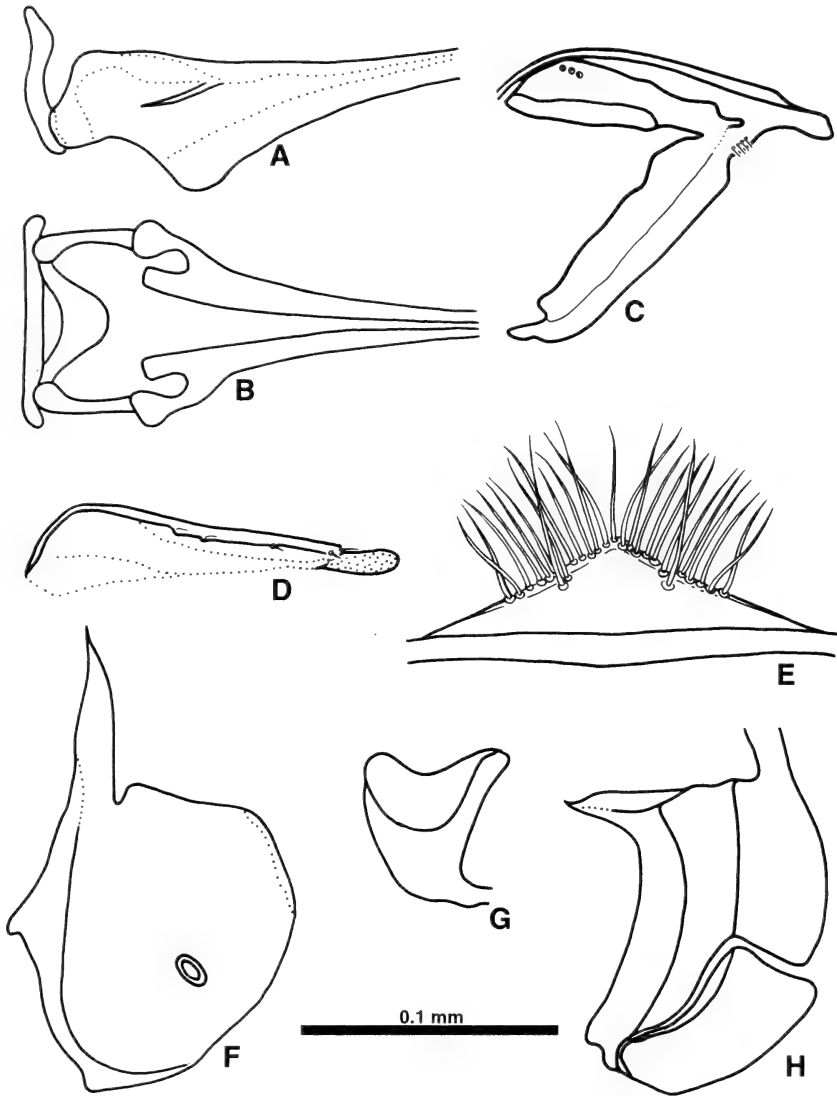


Fig. 5. *Stegomyrmex vizottoi* Diniz, worker sting apparatus. A, sting and furcula in profile; B, sting and furcula in dorsal view; C, oblong plate; D, gonostylus; E, anal plate; F, spiracular plate; G, triangular plate; H, quadrate plate.

Petiole clavate, with anterior peduncle distinct and long, low, rounded node; anteroventral projection vestigial. Postpetiole as broad as long in dorsal view and slightly broader posteriorly than anteriorly, attached to gaster by almost its full width. Gaster somewhat elongate.

*Comments.*—This species is uniquely characterized by the combination of relatively large size (TL  $\geq 6.00$  mm), mesosoma partially sculptured but for the lateral faces which are almost entirely

smooth and shining, and propodeum relatively narrow in dorsal view. *Stegomyrmex vizottoi* is the only species in the genus for which both sexes and castes are known. It has been registered from localities in northern Argentina, Paraguay, and states of Santa Catarina, Paraná, and São Paulo, southeastern Brazil (Fig. 7).

Diniz and Brandão (1993) published observations on the foraging and nesting habits of *Stegomyrmex vizottoi* from Mirasol, São Paulo, Brazil. They observed that



workers are specialized predators of spirabolid millipede eggs and forage solitarily, moving slowly in shaded areas, probing in small cracks and cavities in the soil. The ants seem to use their faces like a shovel, tucking their antennae in the antennal scrobes and pushing soil away with the face. When a millipede egg is found, it is grasped by the undersurface of the mandibles and pressed against the gular face of the worker's head, which then returns to the nest. These ants are virtually unnoticed to the naked eye, not only because they forage individually, but because of their slow movements, and because as they age their integument becomes covered by a thin but hard layer of mud. Moreover, workers can feign death for several minutes when disturbed.

Diniz and Brandão (1993) were the first to examine a *Stegomyrmex* nest in detail. The *S. vizottoi* small and perfectly rounded nest entrance (0.4 cm in diameter) was in a vertical soil bank, leading to a single sinuous tunnel extending about 40 cm to a secondary chamber, in the roof of which they found a funnel leading to the main chamber. Along the tunnel, which had several small dead ends, they found three enlargements, where the returning workers apparently stop to clean the eggs before reaching the secondary chamber. The cleaning process continues at the secondary chamber, and the eggs are piled in the main chamber only when completely cleaned. The main chamber contained the colony dealate gyne, its brood and a pile of fully cleaned millipedes' eggs. The secondary chamber contained the millipede egg shells, never found in the main chamber. The total worker population in this particular nest was 76. A second nest contained some 300 workers, 22 alate gynes, seven dealate gynes, and brood. Colonies transferred to gypsum laboratory nests with conditions and architecture similar to that of natural nests, adapted easily to the new conditions and even constructed the funnel-like structure linking the secondary to

the main chamber. It is interesting to note that in the relatively mild winters in southeastern Brazil, populations of colonies decrease sharply even in the laboratory, and the ants close the nest's entrance, relaying entirely on the millipede eggs collected in the previous season for nutrition during the winter time, the eggs being taken from the pile one at a time, to be consumed by all individuals arranged in a circle. This helps to make these ants unnoticed for several months a year, contributing to their rareness status.

*Examined material* [All deposited in MZSP].—

**BRAZIL: Paraná:** Rio Azul (1.000 m) x.1959 (F. Plaumann) (1 paratype worker) (MZSP collection n. 3147); **Santa Catarina:** Blumenau, P.E. Nascentes (27°06'15"S, 49°09'14"W) (Winkler samples) 30.iii.2001 (Silva, R.R. and Eberhardt, F.) (2 workers); São Bento do Sul, APA Rio Vermelho (26°21'51"S, 49°16'16"W) (Winkler samples) (Silva, R.R. and Eberhardt, F.) (8 workers and 1 gyne); Seara (24°07'S, 52°18'W) (Winkler sample) v-xii.1998 (Rogério R. Silva) (1 worker); **São Paulo:** Anhembi, Faz. Barreiro Rico (in gizzard of *Conopophaga lineata* Wied, 1831) ii.1964 (E. Dante) (MZSP collection n. 3470) (1 paratype worker); Mirassol (collected manually in soil) 10.x.1971 (Diniz, J.L.M.) (MZSP collection n. 11029) (JLMD collection n. 361) (1 paratype worker); xii.1976 (Diniz, J.L.M.) (JLMD collection n. 1226) (2 paratype gynes); 13.ii.1987 (Diniz, J.L.M.) (MZSP collection n. 10924) (1 worker); same data (JLMD collection no. 544), (1 worker); (20° 50'S, 49° 30'W) (nest in soil) 11.xi.1991 (J.L.M. Diniz) (2 workers and 13 males); Ribeirão Preto, Mata Santa Tereza, 10.xii.1985 (C.G. Froelich) (1 worker).

### Accounts of the other *Stegomyrmex* species

#### *Stegomyrmex connectens* Emery, 1912

*Stegomyrmex connectens* Emery, 1912: 51. **Holotype gyne.** PERU: Vilcanota [MCSN] (not examined).

*Comments.*—*Stegomyrmex connectens* is the type species of the genus and remains known only by a single gyne collected in

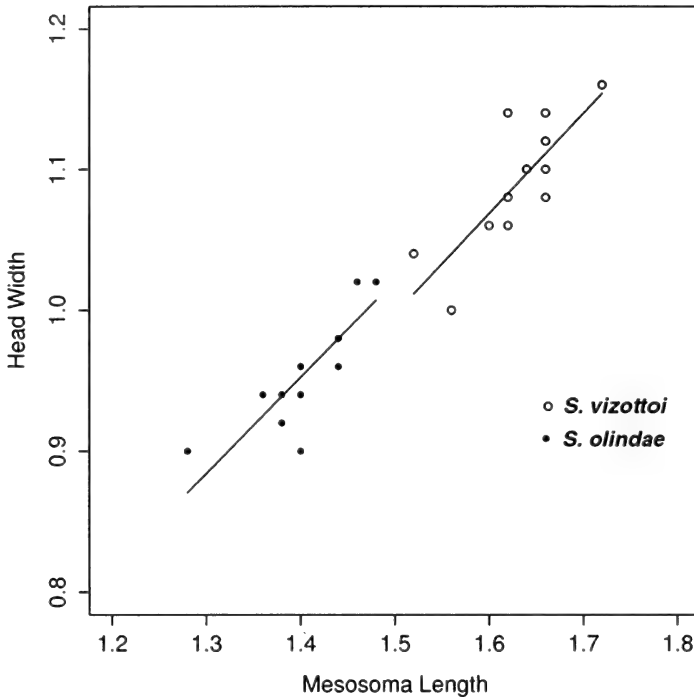


Fig. 6. The relationship between head width and mesosoma length for the worker caste in *S. vizottoi* Diniz and *S. olindae* n. sp. The best-fitting regression line is plotted for each species. There is no significant difference for regression slope or elevation of the two lines. However, there is a significant difference between head width ( $F^{1,28} = 81.554$ ,  $P = 0.000$ ) or mesosoma length ( $F^{1,28} = 163.75$ ,  $P = 0.000$ ) between the species.

Vilcanota, Peru, and a male tentatively assigned to this species, from Mapiri, Bolivia. In the original description, Emery (1912) mentioned that the male might belong to a different *Stegomyrmex* species, although he decided to describe it as *S. connectens*. Diniz (1990) examined this specimen and noticed that it presents some important morphological differences in comparison to the conspecific gyne, mainly in wing venation, pilosity, and by the absence of a second anteroventral spine in the petiolar peduncle. These differences, and the disjunct distribution of the gyne and male specimens, may indicate that they indeed do not belong to the same species.

The gyne of *S. connectens* can be immediately recognized and separated from the other species in the genus by the presence of two anteroventral projections in the petiolar peduncle.

### *Stegomyrmex manni* Smith, 1946

*Stegomyrmex manni* Smith, 1946: 288. **Holotype worker.** PANAMA: Canal Zone, Barro Colorado Island, ix.1941, (James Zetek) (Zetek code 4879) (USNM code 57305) [USNM] (not examined). Serna, 2002: 217 (first record for Colombia).

*Stegomyrmex connectens* Emery, 1912: 101 (in part). Hölldobler and Wilson, 1986: 16 (pilosity features).

**Comments.**—*Stegomyrmex manni* has been registered in the forest floor of mature rainforests in Costa Rica, Panama, and Colombia. The combination of the relatively high promesonotum in side view, propodeal spines directed posteriorly, and propodeal spiracles strongly projected laterally separate this species from the other in the genus.

Hölldobler and Wilson (1986) illustrated and discussed the special soil-binding setae of *S. manni* (cited as *S. connectens*).

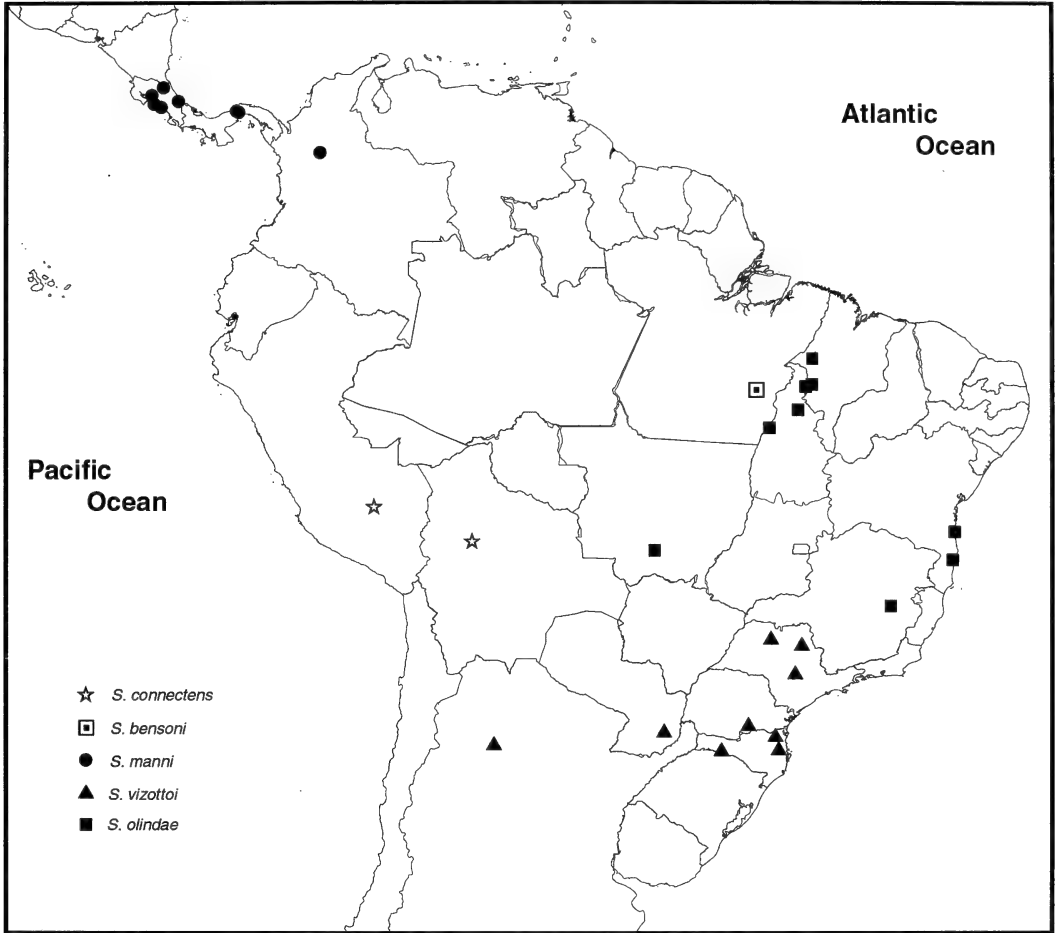


Fig. 7. Distribution map for the known *Stegomyrmex* species.

Longino (2007) published very good pictures of *S. manni* workers. He found specimens of *S. manni* in Winkler samples of sifted litter from the forest floor collected at Manuel Antonio National Park, Carara Biological Reserve, Peñas Blancas east of Monteverde, and Hitoy Cerere Biological Reserve, all in Costa Rica. According to him, Ronald Vargas collected an alate gyne at La Selva Biological Station.

#### ACKNOWLEDGEMENTS

We thank Renata Andrade for depositing in the MZSP ant collection the single known specimen of *S. bensoni*. Lara M. Guimarães took the SEM images and Gláucia Marconato made the *Stegomyrmex bensoni* drawing. Dr. Rogério Rosa da Silva kindly conducted

the statistical tests and prepared Fig. 6; Rosa da Silva and one of us (RMF) collected stegomyrmecine specimens in different expeditions supported by OIKOS Pesquisa Aplicada Ltda; we would like to make a special reference to Dr. Fábio Olmos and Dr. José Fernando Pacheco, who arranged these trips. We would also like to thank several individuals, institutions and agencies that helped or supported other collecting trips that yielded material we studied. The present work was in part supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

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## The Genus *Quartinia* Ed. André, 1884 (Hymenoptera: Vespidae: Masarinae) in Southern Africa. Part II. A New Species with Complete Venation and with a Deeply Excised Antennal Club in the Male

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**Abstract.**—In this publication, the second of a projected series revising the Afrotropical (essentially southern African) species of the genus *Quartinia* Ed. André, 1884 (Hymenoptera: Vespidae: Masarinae), a **new species** with complete venation, *strucki*, is described. By virtue of the similarly deeply excised antennal club of the male, hitherto a character unique to *Q. antennata* Schulthess, a deceptive but superficial similarity to that species is shown. The differences between the two species are discussed.

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The background to the present state of knowledge of the taxonomy of the genus *Quartinia* Ed. André, 1884 and the rationale adopted of publishing a series of papers describing new species as well as reviewing some known species, at a time when a complete revision of the genus is not yet practicable, has been fully stated in Gess (2007). Reference should be made to the introduction of that paper with regard to the size categories adopted to express the relative size of these small wasps.

The acronym AMG stands for Albany Museum, Grahamstown, South Africa.

### DESCRIPTION OF SPECIES AND COLLECTION DATA

#### *Quartinia strucki* Gess, new species

**Diagnosis.**—Large (4.6 – 5.0 mm). Fore wing with *Cu1a* and *2m-cu* complete and as thick as the other veins. Male with deeply excised antennal club, with head and clypeus of usual proportions, and with sternum I bearing a very pronounced, laterally compressed, antero-ventrally directed tubercle. In both sexes tegula with posterior inner corner markedly and acutely inwardly produced.

**Description.**—*Male:* Head and mesosoma black; gaster and legs dark reddish brown. The following are white: basal half of mandible dorsally; labrum, disc of clypeus; paraocular streak up to antennal socket; supraclypeal marking on frons; underside of pedicel and of flagellomeres 1 – 5 (becoming progressively suffused with reddish); small spot on either side of anterior margin of pronotal dorsum and small spot on postero-dorsal angle of same; anterior margin and posterior angle of tegula (otherwise dark brown with a testaceous centre); transverse marking postero-medially on scutellum and entire scutellar lamella; extreme apex of fore trochanter; most of underside and anterior surface of fore femur; anterior surface of fore tibia; distal two thirds of anterior surface of mid femur; anterior surface of mid tibia; most of fore and mid tarsomeres (becoming progressively suffused with reddish). Reddish are: posterior bands, progressively narrower and not reaching sides, on terga I – VI (that on VI reduced to a median spot in one of the specimens); posterior band on tergum II at its ends markedly anteriorly produced to form a sub-circular spot almost reaching anterior margin of tergum; hind tarsomeres. Fore wings lightly browned, especially anteriorly.

Length: circa 4.8 mm; length of fore wing 3.5 mm; hamuli 5.

Head in front view  $1.35 \times$  as wide as long; finely and closely punctured and with microsculptured interstices; matt; frons and vertex with dense, short setae; vertex behind posterior ocelli depressed and occipital carina lamellate medially; POL: OOL =  $1: 0.65$ ; clypeus  $1.4 \times$  as wide as long; its disc evenly convex, its ventral margin broadly hyaline and slightly reflexed; labrum wide, its ventral margin transverse; antenna with all flagellomeres wider than long; first flagellomere  $1.3 \times$  as wide as long; second flagellomere  $1.6 \times$  as wide as long; enlarged club formed of flagellomeres VI – X; flagellomeres VII – IX with a deep, semicircular, sharp edged emargination; flagellomere X unmodified, not part of emargination, forming a convex end to club.

Mesosoma similarly punctured to head, pronotum and mesonotum with dense, short setae.

Terga II and III and to a lesser degree also IV markedly impressed at base, tergum VII with truncate apex and non-hyaline margin, not incised. Sternum I with a very pronounced, laterally compressed, antero-ventrally directed tubercle.

*Female:* Head and mesosoma black; gaster and legs dark reddish-brown. The following are yellowish-white: underside of pedicel and of flagellomeres (becoming progressively suffused with reddish); in some specimens a minute dot on postero-dorsal angle of pronotum; anterior margin and posterior angle of tegula (otherwise dark brown with a testaceous centre); transverse marking postero-medially on scutellum (in some specimens only) and entire scutellar lamella (both tending to be variously suffused with reddish); streak on distal half of fore femur; most of antero-dorsal surface of tibia and basal tarsomere of fore leg; antero-dorsal surface of tibia of middle leg (in some specimens only). Reddish are: most of terga I and II (with exception medial dark markings); posterior bands, progressively narrower and not reaching

sides on terga III and IV. Fore wings lightly browned, especially anteriorly.

Length: 4.6 – 5.0 mm (average of 4: 4.9 mm); length of fore wing 3.6 – 3.7 mm; hamuli 6.

Head in front view  $1.32 \times$  as wide as long; clypeus matt, very finely microreticulate with a scattering of a few minute flat-bottomed punctures; frons and vertex moderately shiny, closely punctured (punctures larger than those of male) and with microsculptured interstices; vertex behind posterior ocelli depressed and occipital carina lamellate medially; POL: OOL =  $1: 0.66$ . Mesosoma shiny; punctures (particularly those on pronotum, mesoscutum and scutellar disc) noticeably larger than on head and in places subconfluent; interstices finely microreticulate. Mesosoma with punctures on terga I and II distinct, especially posteriorly; those on III smaller; all terga finely microsculptured.

*Etymology.*—Named after Dr Michael Struck, botanist and meticulous observer, collector of the material.

*Material examined.*—Holotype: ♂, SOUTH AFRICA: WESTERN CAPE: Farm “Quaggaskop” ( $31^{\circ}19'S$   $18^{\circ}39'E$ ), 30.vii.1992 (M. Struck) (on flowers of *Argyroderma fissum* (Haw.) L. Bol., Aizoaceae: Mesembryanthema) [AMG]. Paratypes: SOUTH AFRICA: WESTERN CAPE: same data as holotype, 1 ♂, 13 ♀♀: same locality but date 1.vi.1993, 1 ♀ (all M. Struck) (all on flowers of *Argyroderma fissum* (Haw.) L. Bol., Aizoaceae: Mesembryanthema) [AMG].

*Geographic distribution.*—Known only from the type locality, the farm Quaggaskop [also spelled Kwaggakop], situated on the Knersvlakte, 31 km due N of Vanrhynsdorp.

*Floral associations.*—*Argyroderma fissum* (Haw.) L. Bol. (Aizoaceae: Mesembryanthema).

*Nesting.*—Unknown.

*Discussion.*—By virtue of the similarly deeply excised antennal club of the male, *Q. strucki* is reminiscent of *Q. antennata* Schulthess, as described by that author

(1935: 388 and unnumbered figure of antenna) and by Richards (1962: 162). The species may be readily distinguished from *Q. antennata*, however, by the following characters – the state of those pertaining to *Q. antennata*, as given in the descriptions and, as ascertained by the present author from examination of the holotype ♂ and of a ♀, being noted in brackets (in Richard's description flagellomere I and flagellomere II are given as segments 3 and 4).

*Q. strucki* is considerably smaller, the length of the male and of the female being circa 4.8 mm and 4.6 – 5.0 mm respectively (6.0 – 7.5 mm and 6.0 mm respectively).

In *Q. strucki* the head of the male,  $1.35\times$  as wide as long, is of usual proportions (head much broader than long).

In *Q. strucki* the clypeus of the male,  $1.4\times$  as wide as long, is of usual proportions and the disc is evenly convex (clypeus very transverse, more than six times as wide as high, raised and sinking almost perpendicularly along whole ventral margin).

In *Q. strucki* the antenna of the male has flagellomere I  $1.3\times$  as wide as long, flagellomere II  $1.6\times$  as wide as long (flagellomere I more than twice as long as broad, flagellomere II quadrate).

In addition to the above characters, in *Q. strucki* sternum I of the male has a very

pronounced, laterally compressed, antero-ventrally directed tubercle (sternum I postero-medially subconically produced).

*Material of Q. antennata Schulthess examined.*—Holotype ♂ [BMNH(E), Hym. 18.52]. SOUTH AFRICA: WESTERN CAPE: Worcester, Sept. – Oct. 1931 (R. E Turner); ♀ [BMNH(E)] SOUTH AFRICA: WESTERN CAPE: Worcester, 3 – 4. x.1928 (R. E. Turner).

#### ACKNOWLEDGMENTS

The following individuals are thanked for much appreciated assistance as specified: Dr Michael Struck for the gift of the specimens here dealt with and for his patience in awaiting their determination; Dr Gavin Broad of the BMNH for the loan of the holotype ♂ and a ♀ of *Quartinia antennata* Schulthess; and Mr Ashley Kirk-Spriggs of the Albany Museum for conveying these specimens from London to Grahamstown.

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## Patterns of Usage of Snail Shells for Nesting by Wasps (Vespidae: Masarinae and Eumeninae) and Bees (Megachilidae: Megachilinae) in Southern Africa

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**Abstract.**—The present contribution to the knowledge of the use of snail shells for nesting by Hymenoptera in southern Africa adds considerably to the earlier contribution by the authors on this subject. It establishes that the strategy of nesting in sand-filled shells is commonly employed by *Quartinia* Ed. André (Vespidae: Masarinae) throughout the sandy winter rainfall areas. It records additional rearings from *Quartinia* nests of *Allocoelia* Mocsáry (Chrysididae), *Tricholabiodes* Radoszkowski and an undescribed genus (Mutillidae), and *Apolysis hesseana* Evenhuis and Greathead (Bombyliidae). Nesting by *Tachysphex hermia* Arnold (Crabronidae: Larrinae) in a sand-filled snail shell is recorded for the first time. It establishes that the distribution of use of snail shells for nesting by bees coincides with and extends along the south coast east of that of *Quartinia*. The bees (Megachilidae: Megachilinae) involved are osmiines, species of *Wainia* (*Caposmia*) Peters and *Hoplitis* (*Anthocopa*) Lepeletier and Serville, and anthidiines, including *Afranthidium* (*Afranthidium*) *hamaticauda* Pasteels, all cavity nesters using empty snail shells. The only other aculeate recorded as using empty shells is *Alastor ricae* Giordani Soika (Vespidae: Eumeninae). Parasitism in bee nests in snail shells is uncommon. Only *Chrysis* Linnaeus (Chrysididae) and Eupelminae (Chalcidoidea: Eupelmidae) were found, each at only two sites. The preferred snail shells are those of several species of *Trigonephrus* Pilsbry (Dorcasidae) on the west coast and in the desertic areas and of *Tropidophora ligata* (Müller) (Pomatidae) along the south coast to the east, all indigenous species. In some areas the habitats of these have been invaded by an exotic snail, *Theba pisana* (Müller) (Helicidae). Shells of this snail are used to a limited extent by the smaller nesters in snail shells. This exotic snail presents a threat to the indigenous snails and to the snail shell nesters. In some areas ongoing coastal development is also a threat.

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The bulk of the knowledge of the use of snail shells for nesting by aculeate Hymenoptera prior to Gess and Gess (1999) was confined to the northern Hemisphere where the use of empty snail shells by bees that do not excavate nesting burrows, but search out pre-existing burrows in which to construct their brood-cells, is widely known and is practised in a variety of habitats by: in the Nearctic two species of Osmiini (*Osmia* and *Ashmeadiella*); and in the Palearctic 14 species of Osmiini (*Osmia* and *Hoplitis*), three in Britain, five in Central Europe, three in the Mediterranean, four in Eurasia and one in Japan, and for one species of Anthidiini, a species of *Rhodanthi-*

*dium*, from the Mediterranean into Asia Minor (Extracted from O'Toole and Raw 1991 and Bellman 1995). Minimal records for southern Africa prior to 1999 were observations, not supported by specimens, of a "Eumenid-wasp" and an "Anthidium-bee" nesting in *Trigonephrus* shells (Hesse 1944) and a record, supported by specimens, of nesting by *Wainia* (*Caposmia*) *elizabethae* (as *Osmia* sp. in Gess and Gess 1988 and as *Hoplitis* sp. in Gess and Gess 1997) in shells of *Tropidophora ligata* collected by Ed. Callan on coastal sand-dunes at Saltvlei, Port Alfred, Eastern Cape.

The 1999 study investigated the use by wasps, bees and spiders of empty and



sand-filled shells of *Trigonephrus* at 10 sites in seven desertic winter-rainfall areas in southern Africa from immediately north of the Orange River east of Oranjemund south to Wallekraal inland of Hondeklip Bay (Gess and Gess 1999). The principal users of the shells were found to be spiders constructing silk-bag nests and two nesting categories of aculeate Hymenoptera: burrow excavators using sand-filled shells, two species of *Quartinia*; and nesters in pre-existing cavities using empty snail shells into which are brought in nesting materials, a eumenine wasp, *Alastor ricae*, and megachilid bees – single species each of *Wainia* (*Caposmia*) (as *Wainia* (*Wainia*) and *Hoplitis* (*Anthocopa*) (Osmiini), and *Afranthidium* (*Afranthidium*) *hamaticauda* (as *Afranthidium* (*Oranthidium*) and in Gess and Gess 2007 as *Afranthidium* (*Afranthidium*) *ablusum*) (Anthidiini). Recorded associates were undescribed *Tricholabiodes* (Mutillidae: Sphaerophthalminae: Dasytabrini), undescribed *Allocoelia* (Chrysididae: Chrysidinae: Allocoeliini) and *Apolysis* (Bombyliidae: Ursiinae: Ursiini) from *Quartinia* nests, Eupelminae (Chalcidoidea: Eupelmidae) reared from cocoons of *H. (Anthocopa)* and *Trichodes aulicus* Kl. (Coleoptera: Cleridae) from a shell used for nesting by *W. (Caposmia)*.

A sample of 13 *Trigonephrus* shells from the Groot Derm in the “Yellow Dunes, part of the northern Succulent Karoo, Northern Cape”, collected by members of the BIO-TA-Southern Africa Project, directed from Hamburg, Germany. From these unopened shells deposited in the Natural History Museum, Berlin, *Hoplitis* sp., *Alastor ricae* and a chrysidid wasp, *Chrysis grootdermensis* Koch emerged (Koch 2006).

Since 1999 the authors have extended their sampling of *Trigonephrus* shells northwards in the winter-rainfall desertic areas of southwestern Namibia to the northern limit of the distribution of the snails (23 additional sites) and southwards, principally along the coast to Cape Town (14 additional sites). Where present they have

investigated the use of the shells of other land snails—an invasive exotic snail *Theba pisana* along the coast from Port Nolloth southwards to Cape Town and eastwards along the south coast to Riet River Mouth in the Eastern Cape Province (15 sites) and an indigenous snail *Tropidophora ligata*, the shells of which were encountered only on the southeastern coast. Neither large numbers of snail shells nor use of snail shells for nesting was discovered in any other areas during the course of fieldwork conducted throughout the semi-arid to arid areas of southern Africa—of particular interest, nowhere in the sandy areas of the Namib Desert north of Lüderitz, or from the Kuiseb River north to Terrace Bay nor in the southern Kalahari, that is desertic areas outside the winter rainfall area. The results of this more extensive study are presented in the present paper together with the earlier contributions giving an account of the present knowledge of nesting by aculeate wasps and bees in snail shells in southern Africa.

Names of authors of taxa are used in the body of the paper only if they are not available from the abstract and appendix.

## METHODS

*Sampling sites.*—The shells of medium to large terrestrial snails, are abundantly available, empty and sand-filled, in the desertic winter rainfall areas and the areas of sandy coastal dunes of southwestern Africa, where they offer abundant secure microhabitats in these areas of sparse low vegetation and unstable, often windswept sand (Figs. 2–5). Generally Asteraceae, Aizoaceae: Mesembryanthema (formerly Mesembryanthemaceae) and monocotyledonous geophytes were represented and in the northern desertic areas generally in addition Geraniaceae (*Sarcocaulon*), Neuradaceae (*Grielum*) and Zygophyllaceae (*Zygophyllum*). Papilionoideae (Fabaceae) were present at some sites. All snail shell sampling sites, except the more eastern ones on the coast lie within the winter

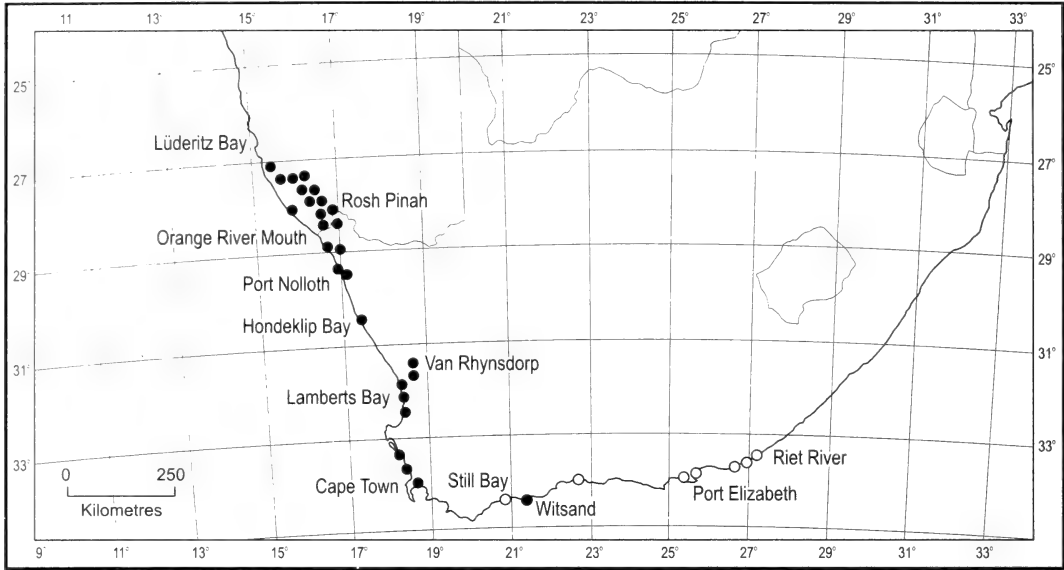


Fig. 1. Distribution of snail shell sampling sites in southern Africa. Solid spots indicate sites at which *Quartinia* (Vespidae: Masarinae) was found nesting in snail shells.

rainfall area. Sampling sites were selected throughout this area (Fig. 1, map, and Appendix, list of all sites with their co-ordinates).

*Identity, size and distributions of snail shells sampled.*—Snail shells sampled were all of terrestrial snails (Mollusca: Gasteropoda) (Figs. 6–11) – several species of



Fig. 2. The Klingartberge, a sparsely vegetated desertic area in southwestern Namibia.



Fig. 3. Near Lutzville southwest of Vanrhynsdorp in the Western Cape, sandveld.



Fig. 4. Donkinsbaai, southwest coast, Western Cape, well vegetated dune slack behind foredunes.



Fig. 5. Witsand, western south coast, sparsely vegetated dunes.

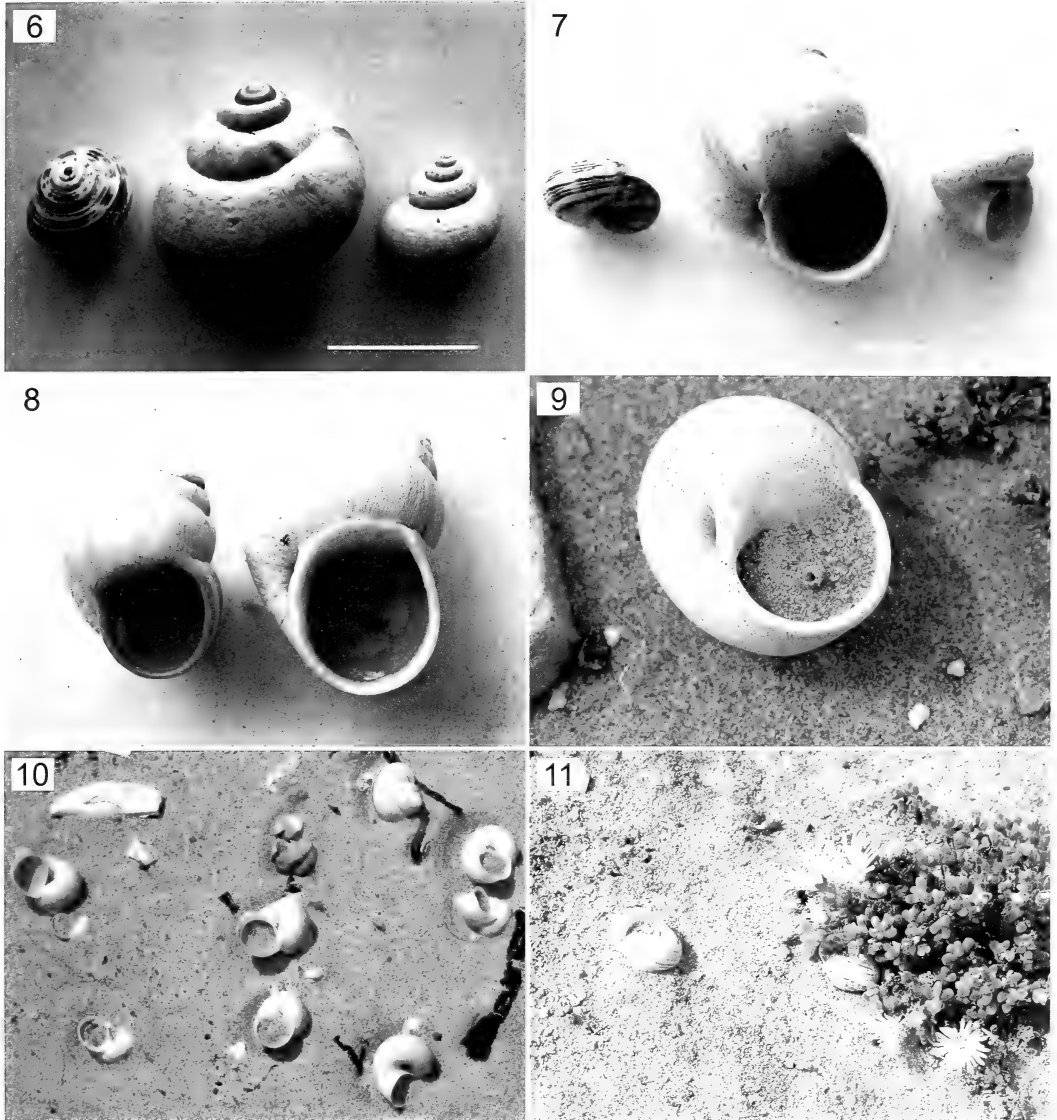
*Trigonephrus* (Dorcasidae), *Tropidophora ligata* (Pomatidae), and an invasive exotic species, *Theba pisana* (Helicidae).

*Trigonephrus* shells are by far the largest with an altitude of 27–44 mm and a major diameter of 24–40 mm (Gess and Gess 1999). *Tropidophora ligata* shells are markedly smaller and therefore offer a cavity of considerably smaller volume but are similarly of greater altitude, 19.7 mm, than major diameter, 16.8 mm (Connolly 1938). *Theba pisana* are also of considerably smaller volume than *Trigonephrus* and in addition differ from both *Trigonephrus* and *Tropidophora* in having a low spiral, the altitude, 12.2 mm, being less than the major diameter, 17.0 mm (Connolly 1938).

In the winter rainfall area in southwestern Namibia and immediately south of the Orange River all snail shells encountered were of *Trigonephrus* and so samples from sites in this area are limited to shells of snails of this genus. At sites in the vicinity of Port Nolloth shells of *Theba pisana* were of equal or even greater abundance and

were also sampled. From Port Nolloth south to Cape Town and east to Riet River in the Eastern Cape *Theba pisana* was abundant. *Trigonephrus* was not encountered east of Cape Town although one species, *Trigonephrus ambiguus* (Fér.), has been recorded as far east as Mossel Bay (Connolly 1938, p. 238). *Theba pisana* was generally abundant to the eastern limit of sampling, at Riet River Mouth in the eastern Cape. *Tropidophora ligata* although recorded from as far west as the Cape Peninsula (Connolly 1938, p. 543) was found no further west than Port Elizabeth in the Eastern Cape, from where it was sampled at sites eastwards to Riet River.

*Theba pisana* is principally coastal Mediterranean in origin but also occurs in Switzerland, Ireland and southwestern Wales and England. It was apparently introduced into Cape Town from Europe circa 1881 (Connolly 1938, p. 269) from where it has spread north along the west coast, east (at least as far as East London, Mary Bursey pers. com.) along the south



Figs 6–11. 6–7, Shells (Mollusca, Gasteropoda) of *Tropidophora ligata* (Pomatiidae), *Trigonephrus* (Dorcasiidae) and *Theba pisana* (Helicidae)  $\times 1$  (scale bar = 2 cm). 8, Shells of two species of *Trigonephrus* to show variation in shell size. 9, Sand-filled shell of *Trigonephrus* showing entrance turret of *Quartinia* (Vespidae: Masarinae). 10, Sand-filled shells of *Tropidophora ligata*. 11, Sand-filled shells of *Theba pisana*.

coast, and in the west has invaded vineyards (Ferreira and Venter 1996) and citrus orchards (Joubert and Du Toit 1998). It has been the subject of considerable study in Israel, southern and western Australia and California, in which areas it is a serious agricultural pest (e.g. Arad and Avivi 1998, Baker 1988, Deisler and Stange 2005). Apart from damaging crops its copious

slime production is considered to make infested plants unpalatable to stock and pollinators.

*Sample size.*—A sample size of 100 shells was chosen, however, sample size taken at some sites was smaller or larger than this number. For example smaller samples of *Trigonephrus* shells resulted from scarcity of shells at sites on the west coast in the

vicinity of Cape Town or from the shortness of collection time for some stops in the Sperrgebiet (Diamond Area no. 1), southwestern Namibia, in which the authors were required to be part of a multidisciplinary group with varied agendas. Larger samples resulted either from the combination of several 100 shell samples from a single site or, in the case of *Theba pisana* and *Tropidophora ligata*, at sites, where incidence of use was very low, particularly along the south coast and eastwards, the decision to take larger samples.

*Sampling method.*—The area of sampling sites was not measured but was approximately 50 m by 50 m. Shells were collected by walking too and fro across the square and progressing from one side to the other. The shell samples were collected into sealed plastic bags. Later live insects which had escaped into the bags were captured and the shells were broken open and the contents examined. Live immatures were reared. Voucher specimens were deposited in the Albany Museum, Grahamstown.

*Condition of material.*—As snail shells in arid areas become bleached but do not degrade it is not possible to establish how long they have been available. Consequently, apart from active nests – nests containing live occupants – it is not possible to establish in what year the nests were constructed. The condition of nest material and dead occupants, however, varies considerably, from some nests being in a very poor or fragmentary state, so that it is clear that in a sample the nests are from a spread of years.

## RESULTS

The results of the study, including published records, are presented in tabular form in the Appendix. Temporary lodgers, those occupants which use the shells only for sleeping and sheltering, have not been included. The present survey, however, confirmed the previous finding (Gess and Gess 1999) that there is a very low incidence of the use of shells for this

purpose in daylight hours even in cold, wet weather. In the calculation of percentage of shells used empty and sandfilled shells are combined and a shell used by more than one occupant is counted only once.

In the desertic area from the Drachenberg in the north to Alexander Bay/Brandkaros in the south 29 sites were sampled. All shells in this area were of *Trigonephrus* species. The percentage of used snail shells ranged from 33% (disregarding one exceptionally low percentage, 8%, obtained from near Kaizer's Camp to a remarkably high 92% (average 50%).

In the coastal sandveld from Port Nolloth in the north to Wallekraal to the south 11 sites were sampled. At all sites samples of *Trigonephrus* shells were taken. The percentage of shells used ranged from 40% to 100% (average 69%). In the Port Nolloth and Hondeklip Bay areas shells of *T. pisana* were present and at some sites were very much more abundant than those of *Trigonephrus*. In a sampling site five kilometres east of Port Nolloth a sample of 125 shells of *T. pisana* was taken with ease but only five shells of *Trigonephrus* were found in the same area. Only 25% of the shells of *T. pisana* had been used but all five *Trigonephrus* shells had been used. Similarly in a sampling site at Hondeklip Bay a sample of 121 *Theba pisana* shells was taken with ease but only 11 shells of *Trigonephrus* were found in the same area. Only 17% of the *T. pisana* shells had been used in contrast to 63% of the *Trigonephrus* shells.

At sites in the sandveld and coastal dune slacks to the south of Vanrhynsdorp south to Cape Town *Trigonephrus* shells were relatively uncommon, increasingly so southwards. The percentage of these shells used was consistently over 50% (56%–71%). Only two of the sites visited were free from *T. pisana*. One was an inland sandveld site southeast of Lutzville and the other was in the coastal dunes at Donkinsbaai. At these sites *Trigonephrus* shells were less common than at most of the northern



sites but more common than at sites infested by *T. pisana*. At Lamberts Bay and a site north of Blaauwberg only nine and seven *Trigonephrus* shells were found but *T. pisana* was very common. Samples of 106, 130 and 134 shells of the latter were investigated. Of these only 18%, 24% and 12% had been used. At Elands Bay and Yzerfontein no *Trigonephrus* shells were found. *Theba pisana* shells were extremely abundant. Of the 147 shells from Elands Bay investigated only 21% had been used and of 200 and 256 shells from Yzerfontein investigated only 9% and 17% had been used.

Along the south and east coasts *Tropidophora ligata* has been recorded from the Cape Peninsula to Maputo (formerly Lorenzo Marques) (Connolly 1938), however, in the present study shells of this snail were found no further west than Port Elizabeth but the invasive exotic *T. pisana* was found to be extremely common in coastal sand dunes along the south coast east to Riet River Mouth, the most eastern site sampled. Use of snail shells along this section of the coast was very patchy. By far the greatest percentage use of *T. pisana* was at Witsand where there had been least disturbance by man but where building development was in full swing. At this site 48% of shells had been used. In the east the percentage of these shells used was 5.34% down to 0%.

Although *T. ligata* shells were abundant at some sites in the east the only site with an appreciable percentage, 19.9%, of used shells was at Kenton-on-Sea in a small area of dune slacks set aside as a bird sanctuary but now neglected and on the edge of housing development. At Salt Vlei, Port Alfred from which the use of these shells by a bee, *Wainia (Caposmia) elizabethae* was first recorded (as *Hoplitis* sp. in Gess and Gess 1988), ongoing building development initiated during the past decade has resulted in the destruction of the dune profile, the natural vegetation and associated snails and insects.

Much habitat destruction in many sandveld and coastal sites from Cape Town north along the west coast at least to Alexander Bay and along the south coast east to East London resulted from the introduction of the Australian *Acacia cyclops* A. Cunn. ex Loudon (Fabaceae: Mimosoideae) in the second half of the nineteenth century for the stabilization of sand flats and coastal dunes (Dennill et al. 1999). In seriously infested areas this shrub has formed extensive monospecific stands entirely replacing the species diverse natural vegetation.

*Sand-filled shells.*—Sand-filled shells in windswept areas offer within the spiral protected sites for the excavation of burrows. This habitat is widely utilized for this purpose by *Quartinia* (Vespidae: Masarinae) in the desertic areas of southwestern Namibia and the western Northern Cape southwards in the sandveld and supra-littoral dunes to Cape Town and eastwards at least to Witsand (Fig. 5). The only other occupant in this category encountered was *Tachysphex hermia* (Crabronidae: Larrinae), however, as only a single instance was recorded, in the Sperrgebiet, it seems that for this wasp this was unusual behaviour. Occasionally a shell used as a pre-existing cavity for nesting by a bee had later filled with sand and been used in addition as a sand-filled shell for nesting by a *Quartinia* (Fig. 17).

In their initial study Gess and Gess (1999) recorded the use of sand-filled snail shells for nesting by two undescribed species of *Quartinia*. Since then Gess (2007) has described seven species collected from nests in snail shells. Representation of species from snail shells was:

- in the desertic winter rainfall area north of the Orange River to south of Lüderitz Bay, *Q. obibensis* and *Q. refugicola* either singly or together;
- in the desertic winter rainfall area south of the Orange River to Hondeklip Bay, *Q. obibensis*, *Q. refugicola* and *Q. conchicola*;

- in sandveld in the vicinity of Hondeklip Bay and Wallekraal, *Q. namaqua* and *Q. namaquensis* (otherwise known only from the Kamiesberg);
- in the sandveld area north of Vanrhynsdorp, *Q. conchicola*;
- in dune slacks along the coast from Donkinsbaai, north of Lamberts Bay, south to 4 km north of Bloubergstrand in the Blaauwberg Conservation Area north of Cape Town, *Q. bonaespei*;
- at Yzerfontein on the southwest coast in addition, surprisingly, *Q. obibensis* and *Q. namaqua*;
- in dune slacks at Witsand on the south Coast east of Cape Town, *Q. australis*.

In the area north of Port Nolloth to south of Lüderitz, in addition to *Q. obibensis* and *Q. refugicola*, a third closely related species *Q. vexillata* Gess was collected from flowers at several sites but was not collected from snail shells. It has been suggested (Gess 2007) that this species most probably also nests in sand-filled snail shells.

All *Quartinia* nesting in snail shells stabilize their nest turrets, burrows and cell walls by the spinning together of sand grains with self-generated silk as first described for *Quartinia vagepunctata* Schulthess (Gess and Gess 1992). Where turrets were present they were of the short vertical or slightly curved form with diameter equal to that of the burrow as described and illustrated in Gess and Gess (1999) (Fig. 9). No species constructing bag shaped turrets such as are constructed by *Q. vagepunctata* (described and illustrated in Gess and Gess 1992) were found. Generally the shaft penetrates deep into the upper part of the spiral of the shell into which the cells are closely packed (Fig. 13), however, in some instances cell construction had been commenced lower in the spiral. The number of cells that can be constructed is limited by the volume of the shell. The number of cells per nest in the large, relatively high *Trigonephrus* shells can therefore be many times the number of

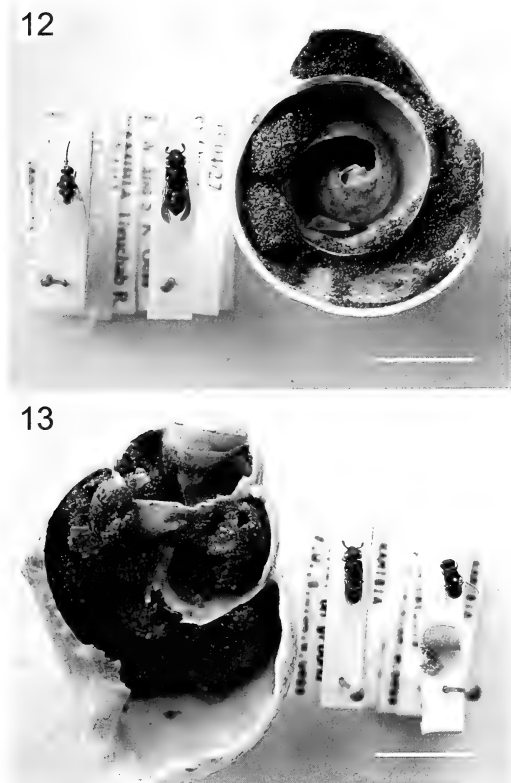
cells per nest in small, relatively low *T. pisana* shells.

All species nesting in snail shells, except *Q. australis* for which no flower visiting records were obtained, visit flowers of "mesems" (Aizoaceae: Mesembryanthema). *Quartinia refugicola*, however, was collected more commonly from flowers of Asteraceae (eight genera) and also from flowers of Zygophyllaceae (*Zygophyllum*), Neuradaceae (*Grielum*) and Geraniaceae (*Sarcocaulon*), all characteristic of the desert areas where it occurs. *Quartinia bonaespei* in addition to "mesems" was collected from flowers of *Trachyandra* (Asphodelaceae) which is a characteristic plant of the supralittoral dunes of the Western Cape. Full flower visiting records are given in Gess (2007). Mating takes place on flowers.

As recorded in Gess and Gess (1999) *Tricholabiodes* sp. (Mutillidae: Sphaerophthalminae: Dasyabriini), an undescribed melanistic species of *Allocoelia* (Chrysidae: Chrysidinae: Allocoeliini) (Fig. 13) and a species of *Apolysis* (Bombyliidae: Usiinae: Usiini) (also in Greathead 1999) (Fig. 12) were reared from nests of *Quartinia* in snail shells from sites in the desertic areas immediately north and south of the Orange River.

Since 1999 further investigation of the "*Tricholabiodes*" specimens has revealed that only one of the specimens, a female, from southwest of Brandkaros was in fact *Tricholabiodes*. Three further females and a female each from southeast of Oranjemund and east of Alexander Bay are not of the genus *Tricholabiodes* but of an undescribed genus (Brothers pers. com. April 2007). Only one additional record of a mutillid, probably of one of these genera, from *Quartinia* cells has been obtained. The new record is for the Drachenberg, the most northern site at which *Trigonephrus* was encountered. It appears that the frequency of occurrence of mutillids in *Quartinia* nests in snail shells is low, only seven records having been obtained from 1,269 nests.





Figs 12–13. 12, Cells and female of *Quartinia obibensis*, and associated *Apolysis hesseana*, adult  $\times 1.5$  (scale bar = 2 cm). 13, Cells and female of *Quartinia refugicola*, and associated *Allocoelia* n. sp., cocoon and imago  $\times 1.5$  (scale bar = 2 cm).

Similarly the only new record of *Allocoelia* from *Quartinia* cells since the rearings from south of Rosh Pinah and east of Port Nolloth is from the Drachenberg. It is probable that it is present throughout the desertic areas to the south and north of the Orange River, however, it would appear that frequency of occurrence of *Allocoelia* in *Quartinia* nests in snail shells is low, only eight records having been obtained from 1,269 nests. *Allocoelia* pupates outside the *Quartinia* cell in which it developed so that in nests from which it has emerged its past presence is readily visible in the form of its empty cocoon attached to the outside of a *Quartinia* cell.

In 1999 the species identity of the *Apolysis* could not be established as only a pharate adult was available. It was

considered that it was probably *A. capicola* Hesse (Greathead 1999). However, subsequent sampling of snail shells has provided adult female and male specimens from *Quartinia* nests from four additional sites from the Orange River north to the Klinghardtberge. The specimens have made it possible to determine the species as *Apolysis hesseana* (Greathead 2006). *Apolysis hesseana* was described briefly from a single denuded female specimen from the Northern Cape (Evenhuis and Greathead 1999) but the new material enabled a full description of the species to be given (Greathead 2006). In nests from which *Apolysis* has emerged the empty pupal cuticle is found attached to the outside of a *Quartinia* cell. It appears that frequency of occurrence of *Apolysis* in *Quartinia* nests in shells is low, only 14 records having been obtained from 1,269 nests but more frequent than by mutillids and *Allocoelia*.

Indeed overall in the areas sampled the frequency of parasitism of *Quartinia* nests in snail shells appears to be low, only 29 records having been obtained from 1,269 nests. It is of interest that no incidents of parasitism were recorded from south of Port Nolloth.

*Empty shells.*—empty snail shells were found to be utilized as nesting cavities by bees throughout the study area. The only other aculeate using the empty shells was *Alastor ricae* (Vespididae: Eumeninae) previously recorded (as “a eumenine”, Gess and Gess 1999) from sites in the vicinity of Brandkaros to the south of the Orange River and presumed to be the same “Eumenid-wasp” referred to by Hesse (1944) as nesting in empty snail shells in “the very arid and sandy belt of the Namib desert”. In subsequent sampling of snail shells by the present authors its nests have been found at 14 sites from north of the Orange River to the Drachenberg and a sample of snail shells collected by the BIOTA-Southern Africa Project at Grootderm to the south of the Brandkaros sites yielded two specimens (Koch 2006). Even

without the presence of the nest builders the nests are readily identified being the only nests in shells with the nest closure constructed from pebbles embedded in a matrix of sand and an unidentified bonding substance (Fig. 14). In samples from which nests of *A. ricae* were obtained the percentage of shells used by this wasp was never more than 4%.

At the majority of sites along the west coast and in the desertic areas in the north the use of *Trigonephrus* shells by bees as nesting cavities was recorded. The percentage of shells used by bees at any one site ranged from 3% to 60%. All nests were of Megachilinae (Megachilidae) of the genera *Wainia* (*Caposmia*), *Hoplitis* (*Anthocopa*) (both Osmiini), *Afranthidium* (*Afranthidium*) (Anthidiini) or an unidentified anthidiine. Very little evidence was found of the use on the west coast of *T. pisana* shells for nesting by any of the bees, for all of which the cavity would be of too small a volume for successful nesting.

Two undescribed species of *Wainia* (*Caposmia*) were reared from nests in snail shells. Both are black with brown setae giving them an overall brownish hue and the gaster an indistinct brown banding, however, they are markedly different in size – Gess sp. C being 7 mm long (average of 5) and Gess sp. A 13 mm long (average of 10). The former was found only in desertic areas north of the Orange River and the latter from south of the Orange River southwards at least to Lamberts Bay. Both of these bees construct petal cells and seal the completed nest with a 5–7.5 mm thick hard, robust wall visible within the mouth of the shell (Gess and Gess 1999) (Figs. 15 and 16). This seal is multi-layered with each layer being constructed from a sheet of petal pieces over which is laid a firm sandy deposit, of which the bonding agent was not established.

One species of *Hoplitis* (*Anthocopa*) (Fig. 17) was reared from nests in snail shells. The cell walls are constructed from petals. Only the petals from a newly

constructed nest in a *Trigonephrus* shell from the site south of Rosh Pinah were identified. They were cut from the pink petals of *Sarcocaulon* (Geraniaceae) (Gess and Gess 1999).

One species of *Afranthidium* (*Afranthidium*), *A. (A.) hamaticauda* Pasteels (Fig. 18), was found sheltering and nesting in *Trigonephrus* shells from the north of the study area south to Wallekraal. Previously (Gess and Gess 1999) the species of *Afranthidium* from snail shells north and south of the Orange River was tentatively identified as *A. (Oranthidium)*, probably *odonturum* Cockerell and that sheltering in *Trigonephrus* shells at Wallekraal as *A. (A.) hamaticauda*. In a subsequent publication the former were erroneously named *Afranthidium (Afranthidium) ablusum* (Cockerell) (Gess and Gess 2007). The nests are readily distinguished from those of Osmiini as they are constructed from white, cottonwool-like, plant fibers (Gess and Gess 1999 and 2007) (Fig. 18). Similar anthidiine nests, but no bees, were in addition found in *Trigonephrus* shells from Lutzville further south.

The second species of anthidiine was found nesting in *Trigonephrus* shells at three sites, at Scorpion Mine, to the northwest of Scorpion Mine and in the Klinghardtberge. The bee is markedly larger than *A. (A.) hamaticauda*, the papillate cocoon being 13.3 mm by 8.1 mm (average of four) compared with 7.7 mm by 4.3 mm (average of three), and the nests are constructed from golden-brown, not white, fibers (Fig. 19).

Along the south coast and to the east percentages of shells used by bees were low overall. Only one species of bee, *Wainia (Caposmia) elizabethae*, 9 mm long (average of 5), considerably smaller than the two western species, black with white setae, giving the gaster a distinct white banding, was recorded from Still Bay in the west to Riet River in the east. Both *T. ligata* and *T. pisana* shells are used, however, those of *T. ligata* for which the highest

percentage use (12.3% at the Kenton-on-Sea bird sanctuary) was recorded seem to be preferred to those of *T. pisana*. It would appear that the low spiral of *T. pisana* is less suitable for nest construction than is the high spiral of *T. ligata*.

There was little evidence of parasitism in bee nests in snail shells. Chrysidid remains were extracted from two osmiine bee nests, one from Drachenberg and one from Aurus. The specimen from Drachenberg was a species of *Chrysis* of the *aestiva* group, possibly *C. grootdermensis*. *Chrysis grootdermensis* was described from one male which, together with eight *Hoplitis* (Megachilidae: Osmiini) and two *Alastor* (Vespidae: Eumeninae), emerged from thirteen *Trigonephrus* shells, which had been collected at Groot Derm in the Richtersveld by members of BIOTA-Southern Africa and deposited in the Museum of Natural History, Berlin, Germany (Koch 2006). Koch suggested that, as the only species of the *aestiva* group, *C. interjecta* Du Buysson, for which biological data are available, emerged from a nest of *Anthidium lituratum* (Megachilidae), the specimen of *C. grootdermensis* might have been from the *Hoplitis* nest.

Numerous Eupelminae (Chalcidoidea: Eupelmidae) emerged from cocoons of *Wainia* (*Caposmia*) sp. C from a *Trigonephrus* shell from a site northeast of Kaiser's Camp and of *Wainia* (*Caposmia*) sp. A from a site southwest of Brandkaros.

*Shells occupied by spiders.*—The only residents, those occupants which not only use the shells as secure sites in which to build nests for rearing young but also "fit them out" as adult residences, were spiders of the families Clubionidae and Salticidae. The former were present at most sites and the latter, ant mimics, most notably at Wallekraal inland of Hondeklip Bay and at sites inland of Port Nolloth.

## DISCUSSION

The shells of medium to large terrestrial snails, which are abundantly available,

empty and sand-filled, in the desertic winter rainfall areas and the areas of sandy coastal dunes of southwestern Africa, offer abundant secure microhabitats in these areas of sparse low vegetation and unstable, often windswept sand. The investigations of such shells by Gess and Gess (1999 and thereafter) were sparked by the exciting discovery of nesting in sand-filled shells by ground nesting, silk-spinning *Quartinia* (Vespidae: Masarinae), representing a unique strategy for survival by a ground nester in such a habitat.

Although in windswept sandy areas, where the ground is unstable, sand-filled snail shells represent the only microhabitat offering a secure nesting site for *Quartinia*, where rock outcrops occur, pockets of sand offer additional secure nesting sites. That such sites may be used by snail shell nesters was confirmed by the discovery of *Q. refugicola* nesting in sand trapped in calcrete in addition to sand trapped in *Trigonephrus* shells (Gess and Gess 1999). It is therefore clear that for *Q. refugicola*, at least, nesting in snail shells is not obligatory. It seems probable that this will be found to be the case for at least some of the other species collected from nests in snail shells.

The use of empty snail shells as pre-existing nesting cavities by osmiines is known from the Nearctic, Palaearctic, Britain, Central Europe, the Mediterranean, Eurasia and Japan and by an anthidiine from the Mediterranean into Asia Minor (O'Toole and Raw 1991, Bellman 1995) in a variety of habitats. The use of empty snail shells by aculeates (osmiines, anthidiines and a eumenine) in the desertic and coastal areas of southern Africa does not therefore represent a desert survival strategy. It is, however, of note that nesters of this category were found to be more diverse and more abundant in the winter rainfall desertic areas than they were in the coastal areas.

Not surprising is the wide use of shells as lodgings and nesting sites by spiders.

14



15



16



17



18



19



Figs 14–19. 14, *Alastor ricae* (Vespidae:Eumeninae) with pebble and matrix cell closure in cut open *Trigonephrus* shell  $\times 1.5$  (scale bar = 2cm). 15, *Wainia* (*Caposmia*) species A (Megachilinae: Osmiini) and nest entrance closure with exit hole  $\times 1.6$  (scale bar = 2 cm). 16, Nest of *Wainia* (*Caposmia*) species A with nest closure removed to one side. 17, *Hoplitis* (*Anthocopa*) sp. (Megachilinae: Osmiini) and *Quartinia refugicola* with cut open shell of *Trigonephrus* to show a cell of the former in the peek of the spiral followed by cells of the latter  $\times 1.5$  (scale bar = 2 cm). 18, *Afranthidium* (*Afranthidium*) *hamaticauda* (Megachilinae: Anthidiini) with white plant fiber nest in cut open *Trigonephrus* shell  $\times 2$  (scale bar = 2 cm). 19, Anthidiine species 2 with cocoon and nest in cut open *Trigonephrus* shell  $\times 1.5$ .

Spiders are not always the initial occupiers of shells but in many instances were found to have moved into shells already occupied by wasps or bees, which were either actively nesting or had completed nesting. Clearly, when nesting was still in progress, the occupation by a spider will have terminated nesting and, when nests had been completed but emergence of offspring had not yet taken place, presence of a spider will have been hazardous for exiting by imagines. Considering that in the desert where a sea mist rolls in from the west coast in the evenings and persists well into the morning and where the mid-day heat is often extreme it is surprising that the use of the shells for sheltering during these times seems to be minimal. Also surprising is the low level, in most areas, of parasitism of the wasps and bees by insects feeding on the immatures or the provision.

Clearly, the marked difference in volume of the large shells of *Trigonephrus* with a western distribution and the much smaller shells of *Tropidophora ligata* with a southern to eastern distribution must make a difference to the suitability of the cavity offered. This may explain the greater percentages of shells used and the larger number of bee species and *Quartinia* species using shells where *Trigonephrus* shells are available as compared to the south and southeast where they are not available. This possibility is supported by the fact that where the invasive snail *Theba pisana*, having shells with a relatively small volume and low spiral, has all but replaced *Trigonephrus* percentage use of *T. pisana* is very low compared with *Trigonephrus*. Indeed in areas of increasing abundance of *T. pisana* at the expense of *Trigonephrus* a drop in populations of snail shell users may be expected, which would in all probability adversely affect pollination of at least some of the plants visited and thus have a cascade effect. In addition in some areas ongoing spread of *Acacia cyclops* and coastal development pose a threat both to snails and snail shell nesters as it forms

monospecific stands which replace the diverse natural vegetation on which they depend.

The division of snail shells into empty and sand-filled does not suggest that either state has any permanence. In windswept sandy areas the duration of either state is dictated by the intervals between gale force winds. During these quiet periods cavity nesting wasps or bees will seek out empty shells in which to nest and excavators in friable soil will seek out suitable sites for nesting. It is clear from the survey that the only regular nesters in this latter category are *Quartinia* species and that their nests are commonly found in snail shells throughout the winter rainfall desertic areas, at some sites in the sandveld and at many in the coastal dune slacks on the west coast and along the south coast eastwards at least as far as Still Bay. The probable explanation is their ability to spin silk. In nest building the silk is initially used to stabilize sand grains in the excavation of a burrow and the construction of a nest turret. The silk lined burrow reaches far into the shell where cell construction from sand and silk takes place safely in the spiral of the shell where the cells can be securely packed and attached to the shell. As is clear from shells collected into plastic bags, the sand matrix is often not stable and easily falls out of the shells together with the entrance turret and burrow. Thus when the next gale blows, tumbling the shells, some at least of the sand-filled shells containing *Quartinia* cells will empty of all but the cells and some at least of the empty shells containing the nests of cavity nesting wasps and bees will fill with sand. It is therefore not surprising that in some shells a few bee cells were found in the peak of the spiral followed by *Quartinia* cells and in others a few *Quartinia* cells were found in the peak followed by bee cells. Furthermore, *Quartinia* cells found in otherwise empty shells do not suggest that the builder, like the cavity nesters, brought building materials into an empty shell. In

the earlier investigation two species of *Quartinia* were found to be involved. In the present survey seven species have been found nesting in this way. However, it is of note that in some areas where one or more of these *Quartinia* species has been found nesting in snail shells additional species, not found nesting in shells, have been collected visiting flowers. These were all species with incomplete venation, formerly of the genus *Quartinoides* Richards now included in *Quartinia* (following van der Vecht and Carpenter 1990). In all instances this was where rocky outcrops were present or the vegetation was less sparse.

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Taxa in order of table headings: -

Shell ID (Mollusca, Gasteropoda): Dorcasiidae – *Trigonephrus* Pilsb. (Figs. 6–9); Pomatiidae – *Tropidophora ligata* (Müll) (Figs. 6, 7 and 10); Helicidae – *Theba pisana* (Müll) (Figs. 6, 7 and 11).

Masarinae (Vespidae): *Quartinia* Ed. André, *australis* Gess, *bonaespei* Gess, *conchicola* Gess, *namaqua* Gess, *namaquensis* Gess, *obibensis* Gess (Fig. 12), *refugicola* Gess (Fig. 13).

Chrysididae: A. = *Allocoelia* n. sp. (Fig. 13), C. g. = *Chrysis grootdermensis* Koch; C. ? g. = *Chrysis* (aestiva group) ? *grootdermensis*;

Bombyliidae: *Apolysis hesseana* Evenhuis and Greathead (Fig. 12).

Eumeninae (Vespidae): *Alastor ricae* Giordani Soika (Fig. 14).

Mutillidae: T. = *Tricholabiodes* n. sp.; n. genus.

Megachilidae, Megachilinae: Osmiini – W. (C.) = *Wainia* (*Caposmia*) Peters, W. (C.) e. = W. (C.) *elizabethae* Brauns, W. (C.) sp. A, W. (C.) sp. C. (Figs. 15 and 16) and H. (A.) = *Hoplitis* (*Anthocopa*) Lepeletier and Serville (Fig. 17); Anthidiini – A.(A.) h. = *Afranthidium* (*Afranthidium*) *hamaticauda* Pasteels (Fig. 18) and anthidiine sp. 2 (Fig. 19).

Spiders: Clubionidae and Salticidae

Additional taxa: -

\*Crabronidae: Larrinae: *Tachysphex hermia* Arnold; \*\* Eupelminae (Chalcidoidea: Eupelmidae) from cocoons of *Wainia* (*Caposmia*).

## APPENDIX

Available data on the use of snail shells in the semi-arid to arid areas of southern Africa. Collectors' numbers are those of

Appendix.

| Site<br>collectors' no.               | Shall ID<br>no & % used | Masarinae nesting<br>in sand-filled shells | Chrysididae<br>"parasites"     | Bombyliidae<br>"parasites" | Mutillidae<br>"parasites"   | Megachilidae nesting in<br>empty snail shells | Eumeninae nesting in<br>empty snail shells | Spiders<br>residents |
|---------------------------------------|-------------------------|--|--------------------------------|----------------------------|-----------------------------|---|--|----------------------|
| Drachenberg seaward<br>side           | Trigonephrus            |  | C.?g. in<br>megachilid<br>nest |                            | 1 ♀ ex<br>Quartinia<br>cell |   |  |                      |
| 27.05S 15.25E<br>05/06/21             | 90 70%                  | 50 55.6%                                   | 1                              |                            |                             | 9 10%   | 4 4.4%                                     | 12 13.3%             |
| Drachenberg landward<br>side          | Trigonephrus            |  | A. in Quartinia<br>nest        |                            |                             |   |  |                      |
| 27.05S 15.25E<br>05/06/15             | 44 60%                  | 17 38.6%                                   | 1                              |                            |                             |   |  |                      |
| Sperrgebiet main rd<br>27.14S 15.28E* | Trigonephrus            |  |                                |                            |                             | 8 18.2%                                       | 2 4.5%                                     | 6 13.6%              |
| 02/03/6a                              | 29 65.5%                | 10 34%                                     |                                |                            |                             | A. (A.) h.<br>? W. (C.)<br>? H. (A.) 4 13.8%  |  | 7 24%                |
| W Klinghardtberge<br>NW Heioab        | Trigonephrus            | obibensis                                  |                                |                            |                             |   |  |                      |
| 27.17S 15.36E<br>03/04/64             | 61 63.9%                | 34 55.7%                                   |                                |                            |                             | 2 3.3%  | 1 1.6%                                     | 17 27.9%             |
| Klinghardt's Basin<br>27.19S 15.46E   | Trigonephrus            | obibensis + refugicola                     |                                |                            |                             | anthidine 2                                   |  |                      |
| 05/06/24                              | 60 66.7% used           | 30 50%                                     |                                | 1                          |                             | 13 21.7%                                      | 1 1.6%                                     |                      |
| Klinghardtberge<br>27.19S 15.46E      | Trigonephrus            | obibensis                                  |                                |                            |                             | W. (C.) sp. C                                 |  |                      |
| 05/06/29                              | 53 75.5%                | 37 69.8%                                   |                                |                            |                             | 13 24.5%                                      |  |                      |
| Klinghardtberge<br>27.19S 15.47E      | Trigonephrus            |  |                                |                            |                             | ?   |  |                      |
| 05/06/34                              | 36 91.7%                | 30 83.3%                                   |                                |                            |                             | 10 27.8%                                      |  |                      |
| Sperrgebiet main rd<br>27.23S 15.32E  | Trigonephrus            |  |                                |                            |                             | ? W. (C.)<br>? H. (A.)                        |  |                      |
| 02/03/7a                              | 19 63.2%                | 6 31.6%                                    |                                |                            |                             | 4 21.1%                                       | 2 10.5%                                    |                      |
| Nomitsas<br>27.27S 15.52E             | Trigonephrus            | refugicola                                 |                                |                            |                             | ? W. (C.)<br>? H. (A.)                        |  |                      |
| 02/03/21                              | 32 65.6%                | 13 40.6%                                   |                                |                            |                             | 11 34.4%                                      |  |                      |
| SE Heioab<br>27.27S 16.06E            | Trigonephrus            |  |                                |                            |                             |   |  |                      |
| 03/04/48                              | 30 70%                  | 19 63.3%                                   |                                |                            |                             | 7 23.3%                                       | 1 3.3%                                     |                      |



Appendix. Continued.

| Site<br>collectors' no. | Shell ID<br>no & % used | Masarinae nesting<br>in sand-filled shells | Chrysidae<br>"parasites" | Bombyliidae<br>"parasites" | Mutillidae<br>"parasites" | Megachilidae nesting in<br>empty snail shells | Eumeninae nesting in<br>empty snail shells | Spiders<br>residents |
|-------------------------|-------------------------|--|--------------------------|----------------------------|---------------------------|---|--|----------------------|
| Othona "forest"         |                         |  |                          |                            |                           |   |  |                      |
| 27.29S 16.10E           | Trigonephrus            |  |                          |                            |                           | (mud walls - 1 0.5%                           |  |                      |
| 03/04/47                | 223 36.8%               | 79 35.4%                                   |                          | 1 0.5%                     |                           | 8 3.6%  | 1 0.5%                                     |                      |
| nr Kaizer's Camp        | Trigonephrus            | obibensis                                  |                          |                            |                           |   |  |                      |
| 27.30S 15.44E**         | 88 8%                   | 4 4.5%                                     |                          |                            |                           | 3 3.4%  |  |                      |
| 05/06/22&23             | Trigonephrus            | refugicola                                 |                          |                            |                           |   |  |                      |
| Uguchab River bed       | 27.31S 16.12E           | 103 45.4%                                  |                          |                            |                           | 35 15.4%                                      | 4 1.8%                                     | 2 0.8%               |
| 03/04/43                | 227 54%                 |  |                          | 7 3.1%                     |                           |   |  |                      |
| Aurus                   | Trigonephrus            |  | chrysidid in<br>bee nest |                            |                           |   |  |                      |
| 27.36S 16.22E           |                         | 53 36.6%                                   | 2                        |                            |                           | 43 29.7%                                      | 1 0.7%                                     | 5 3.4%               |
| 03/04/37                | 145 57.2%               |  |                          |                            |                           |   |  |                      |
| E Aurus                 | Trigonephrus            |  |                          |                            |                           |   |  |                      |
| 27.36S 16.23E           |                         | 66 58.41%                                  |                          |                            |                           | 9 7.96%                                       |  |                      |
| 03/04/38                | 113 62.8%               |  |                          |                            |                           | (mud walls - 8 4.9%)                          |  |                      |
| E Aurus                 | Trigonephrus            |  |                          |                            |                           |   |  |                      |
| 27.37S 16.25E           |                         |  |                          |                            |                           | 37 22.7%                                      | 2 1.2%                                     |                      |
| 03/04/39                | 53 32.5%                |  |                          |                            |                           |   |  |                      |
| Channaub                | Trigonephrus            |  |                          |                            |                           |   |  |                      |
| 27.43S 16.05E           |                         | 9 45%                                      |                          |                            |                           |   |  | 12 60%               |
| 02/03/8                 | 20 85%                  |  |                          |                            |                           | ? W. (C.)                                     |  |                      |
| Channaub                | Trigonephrus            |  |                          |                            |                           | ? H. (A.)                                     |  |                      |
| 27.43S 16.05E           |                         | 7 35%                                      |                          |                            |                           | 6 30%   |  | 7 35%                |
| 02/03/12                | 20 70%                  | obibensis                                  |                          |                            |                           | anthidiine 2                                  |  |                      |
| NW Scorpion Mine        | Trigonephrus            |  |                          |                            |                           |   |  |                      |
| 27.45S 16.32E           |                         | 54 52.9%                                   |                          | 3 2.9%                     |                           | 15 14.7%                                      |  | 8 7.8%               |
| 03/04/35                | 102 58.8%               | obibensis                                  |                          |                            |                           | anthidiine 2                                  |  |                      |
| Scorpion Mine           | Trigonephrus            |  |                          |                            |                           |   |  |                      |
| 27.49S 16.35E           |                         | 29 27.6%                                   |                          |                            |                           | 13 12.3%                                      |  |                      |
| 03/04/33                | 105 55.2%               |  |                          |                            |                           |   |  |                      |
| Red Dune, Obib          | Trigonephrus            |  |                          |                            |                           |   |  |                      |
| 27.55S 16.39E           |                         | 7 7%                                       |                          |                            |                           | 12 12%  | 1 1%                                       | 1 1%                 |
| 03/04/32                | 100                     | obibensis                                  |                          |                            |                           |   |  |                      |
| Obib hut site           | Trigonephrus            |  |                          |                            |                           |   |  |                      |
| 28.00S 16.39E           |                         | 100 58.8%                                  |                          |                            |                           | 33 19.4%                                      | 3 1.8%                                     | 8 4.7%               |
| 03/04/27                | 170 73.1%               |  |                          |                            |                           |   |  |                      |

Appendix. Continued.

| Site<br>collectors' no.                                  | Shell ID<br>no & % used                  | Masarinae nesting<br>in sand-filled shells   | Chrysididae<br>"parasites"   | Bombyliidae<br>"parasites" | Mutillidae<br>"parasites"   | Megachilidae nesting in<br>empty snail shells   | Eumecinae nesting in<br>empty snail shells | Spiders<br>residents |
|--|--|--|------------------------------|----------------------------|---|---|--|----------------------|
| SSW Boegoeborg<br>28.00S 15.52E<br>02/03/16              | Trigonephrus<br>55 72.7%                 | 17 30.9%                                     |                              |                            |   | A. (A.) h.<br>? W. (C.)<br>? H. (A.)  | 1 1.8%                                     | 11 20%               |
| S Rosh Pinah<br>28.03S 16.51E<br>96/97/59/61, 63-77      | Trigonephrus<br>17 100%                  | refugicola +<br>obibensis                    | A. in Quartinia<br>nest<br>3 |                            |   | 8 14.5%<br>?H. (A.) sp. 1<br>?W. (C.)<br>1  |  |                      |
| S Rosh Pinah<br>28.03S 16.51E<br>96/97/60, 62, 78-81, 84 | Sand filled cavities in<br>calcrete<br>6 | refugicola<br>7                              | A. in Quartinia<br>nest<br>3 |                            |   |   |  |                      |
| Red Dune, Obib<br>28.08S 16.42E<br>03/04/29              | Trigonephrus<br>118 46.6%                | refugicola<br>43 36.4%                       |                              |                            |   | 16 13.6%<br>W. (C.) sp. C   |  |                      |
| Red Dune, Obib<br>28.08S 16.42E<br>03/04/30              | Trigonephrus<br>104 67.3%                | refugicola<br>39 37.5%                       |                              |                            |   | 36 34.6%<br>? W. (C.)<br>? H. (A.)<br>2 15.4%<br>A. (A.) h.<br>H. (A.) sp. 1<br>5 11.1%<br>W. (C.) sp. A<br>H. (A.) sp. 1<br>7 14.9%<br>W. (C.) sp. A | 3 2.9%                                     | 5 4.8%               |
| E Oranjemund<br>28.26S 16.42E<br>97/98/67                | Trigonephrus<br>13 84.6%                 | refugicola<br>11 84.6%                       |                              | 1 7.7%                     |   |   |  |                      |
| SW Brandkaros<br>28.29S 16.40E<br>96/97/99-108A          | Trigonephrus<br>36 75%                   | refugicola<br>14 38.9%                       |                              |                            |   |   | 1 2.8%                                     | 1 2.8%               |
| SW Brandkaros<br>28.29S 16.40E**<br>96/97/131-152        | Trigonephrus<br>47 89.4%                 | refugicola<br>obibensis conchicola<br>31 66% |                              |                            |   |   | 1 2.1%                                     | 5 10.6%              |
| SW Brandkaros<br>28.29S 16.40E<br>96/97/160-162          | Trigonephrus<br>23 78.3%                 | 13 56.5%                                     |                              |                            | T. ex<br>Quartinia<br>cell 1 ♀<br>new<br>genus<br>Ex Quartinia<br>cells 3 ♀ | 8 34.8%   | 2 8.7%                                     |                      |
| E Oranjemund<br>28.30S 16.36E<br>97/98/36                | Trigonephrus<br>73 43.8%                 | refugicola<br>23 31.5%                       |                              |                            |   | A. (A.) h.<br>? W. (C.)<br>? H. (A.)<br>5 6.8%  |  |                      |

Appendix. Continued.

| Site<br>collectors' no. | Shell ID<br>no & % used | Masarinae nesting<br>in sand-filled shells | Chrysididae<br>'parasites' | Bombyliidae<br>'parasites' | Mutillidae<br>'parasites' | Megachilidae nesting in<br>empty snail shells | Eumeninae nesting in<br>empty snail shells | Spiders<br>residents |
|-------------------------|-------------------------|--|----------------------------|----------------------------|---------------------------|---|--|----------------------|
| SE Oranjemund           | Trigonephrus            | conchicola                                 |                            |                            | new genus<br>Ex Quartina  | A. (A.) h.                                    |  |                      |
| 28.35S 16.30E           | 4                       | 2  |                            |                            | cells 1 ♀                 | 1   |  |                      |
| 96/97/95-98             | Trigonephrus            |  | C. g.                      |                            |                           | Hoplitis sp.                                  |  |                      |
| Groot Derm              |                         |  |                            |                            |                           |   |  |                      |
| NE Alexander Bay        |                         |  |                            |                            |                           |   |  |                      |
| 28.37S 16.40E           | 13                      |  | 1 emerged                  |                            |                           |   | 2 emerged                                  |                      |
| BIOTA-SA                | Trigonephrus            |  |                            |                            | new genus<br>ex Quartina  | 8 emerged<br>A. (A.) h.                       |  |                      |
| E Alexander Bay         | 4                       | 3  |                            |                            | cells 1 ♀                 | 1   |  |                      |
| 28.38S 16.28E           | Trigonephrus            | refugicola                                 |                            |                            |                           | A. (A.) h.                                    |  |                      |
| 96/97/95-98             | 14                      | 5  |                            |                            |                           | 3   |  | 2                    |
| N Port Nolloth          | 78.6%                   | conchicola                                 |                            |                            |                           | 21.4%   |  | 14.3%                |
| 28.47S 16.38E           | Trigonephrus            |  |                            |                            |                           |   |  |                      |
| 97/98/77B               |                         |  |                            |                            |                           |   |  |                      |
| N Port Nolloth          |                         |  |                            |                            |                           |   |  |                      |
| 28.50S 16.40E           | 25                      | 7  |                            |                            |                           |   |  |                      |
| 96/97/169               | 40%                     | 28%  |                            |                            |                           |   |  | 8%                   |
| 5km E Port Nolloth      | Theba pisana            |  |                            |                            |                           |   |  |                      |
| 29.15S 16.53E           | 125                     | 19   |                            |                            |                           |   |  |                      |
| 05/06/81                | 24.8%                   | 15.2%                                      |                            |                            |                           |   |  | 9.6%                 |
| 5km E Port Nolloth      | Trigonephrus            |  |                            |                            |                           |   |  |                      |
| 29.15S 16.53E           | 5                       | 1  |                            |                            |                           |   |  |                      |
| 05/06/82                | 100%                    | 15%  |                            |                            |                           |   |  |                      |
| Port Nolloth            | Trigonephrus            |  |                            |                            |                           |   |  |                      |
| 29.16S 16.53E           | 26                      | 6  |                            |                            |                           |   |  |                      |
| 05/06/83                | 53.8%                   | 23%  |                            |                            |                           |   |  |                      |
| Port Nolloth            | Theba pisana            |  |                            |                            |                           |   |  |                      |
| 29.16S 16.53E           | 64                      | 3  |                            |                            |                           |   |  |                      |
| 05/06/83                | 14.1%                   | 4.6%                                       |                            |                            |                           |   |  |                      |
| Port Nolloth            | Trigonephrus            |  |                            |                            |                           |   |  |                      |
| 29.16S 16.53-54E        | 10                      | 1  |                            |                            |                           |   |  |                      |
| 05/06/89                | 80%                     | 10%  |                            |                            |                           |   |  |                      |
| E Port Nolloth          | Trigonephrus            |  |                            |                            |                           |   |  |                      |
| 29.16S 16.54E           | 86                      | 23   |                            |                            |                           |   |  |                      |
| 05/06/84                | 38.4%                   | 26.7%                                      |                            |                            |                           |   |  | 9.3%                 |

Appendix. Continued.

| Site<br>collectors' no. | Shell ID<br>no & % used | Mesariinae nesting<br>in sand-filled shells | Chrysididae<br>'parasites' | Bombyliidae<br>'parasites' | Mutillidae<br>'parasites' | Megachilidae nesting in<br>empty snail shells | Eumecinae nesting in<br>empty snail shells | Spiders<br>residents |
|-------------------------|-------------------------|---|----------------------------|----------------------------|---------------------------|---|--|----------------------|
| F Port Nolloth          | Trigonephrus            |   | A.<br>in Quartinia<br>nest |                            |                           |   |  |                      |
| 29.16S 16.55E           |                         |   | 1 5.6%                     |                            |                           |   |  |                      |
| 97/98/79                | 18 50%                  | 4 22.2%                                     |                            |                            |                           | ?   |  | 2 11.1%              |
| 6km E Port Nolloth      | Trigonephrus            |   |                            |                            |                           |   |  |                      |
| 29.16S 16.55E           |                         |   |                            |                            |                           |   |  |                      |
| 05/06/78                | 28 82.1%                | 12 42.9%                                    |                            |                            |                           | 7 25%   |  | 16 57.1%             |
| E Hondeklip Bay         | Trigonephrus            | namaqua                                     |                            |                            |                           | ? osmiine                                     |  |                      |
| 30.19S 17.17E           |                         |   |                            |                            |                           |   |  |                      |
| 05/06/87                | 11 63.6%                | 5 45.5%                                     |                            |                            |                           | 3 27.3%                                       |  |                      |
| E Hondeklip Bay         | Theba pisana            | namaqua                                     |                            |                            |                           | ? osmiine                                     |  |                      |
| 30.19S 17.17E           |                         |   |                            |                            |                           |   |  |                      |
| 05/06/87                | 121 17.4%               | 9 7.4%                                      |                            |                            |                           | 3 2.5%  |  | 10 8.3%              |
| W Wallekraal            | Trigonephrus            | namaquensis<br>conchicola                   |                            |                            |                           | anthidiine                                    |  |                      |
| 30.21S 17.26E           |                         | 15  |                            |                            |                           |   |  |                      |
| 97/98/146               | 58 84.5%                |   |                            |                            |                           | 22  |  | 9                    |
| W Wallekraal            | Trigonephrus            |   |                            |                            |                           | A. (A.) h.                                    |  |                      |
| 30.22S 17.27E           |                         |   |                            |                            |                           | W. (C.) sp.A                                  |  |                      |
| 97/98/143               | 79 81%                  | 12 15.2%                                    |                            |                            |                           | 44 55.7%                                      |  | 8 10.1%              |
| W Wallekraal            | Trigonephrus            | namaqua                                     |                            |                            |                           | W. (C.) sp. A                                 |  |                      |
| 30.22S 17.28E           |                         |   |                            |                            |                           |   |  |                      |
| 05/06/88                | 60 93.3%                | 12 20%                                      |                            |                            |                           | 36 60%  |  | 26 43.3%             |
| N Vantrhynsdorp         | Trigonephrus            |   |                            |                            |                           | ? W. (C.)                                     |  |                      |
| 31.30S 18.43E           |                         |   |                            |                            |                           |   |  |                      |
| 96/97/178               | 34 71.4%                | 4 11.8%                                     |                            |                            |                           | 1 2.9%  |  | 7 20.6%              |
| N Vantrhynsdorp         | Trigonephrus            | conchicola                                  |                            |                            |                           | ? osmiine                                     |  |                      |
| 31.31S 18.43E           |                         |   |                            |                            |                           |   |  |                      |
| 05/06/90                | 127 39.4%               | 38 29.9%                                    |                            |                            |                           | 4 3.1%  |  | 8 6.3%               |
| N Vantrhynsdorp         | Trigonephrus            |   |                            |                            |                           |   |  |                      |
| 31.31S 18.43E           |                         |   |                            |                            |                           |   |  |                      |
| 05/06/90                | Small                   |   |                            |                            |                           |   |  |                      |
| SE Lutzville            | Trigonephrus            | c 6 10.2%                                   |                            |                            |                           | anthidiine                                    |  | c 6 10.2%            |
| 31.36S 18.23E           |                         | conchicola                                  |                            |                            |                           |   |  |                      |
| 05/06/98                | 59 61%                  | 10 16.9%                                    |                            |                            |                           | 12 20%  |  | 14 23.7%             |

Appendix. Continued.

| Site<br>collectors' no. | Shell ID<br>no & % used | Maarinae nesting<br>in sand-filled shells | Chrysidae<br>"parasites" | Bombyliidae<br>"parasites" | Mutillidae<br>"parasites" | Megachilidae nesting in<br>empty snail shells | Eumeninae nesting in<br>empty snail shells | Spiders<br>residents |
|-------------------------|-------------------------|---|--------------------------|----------------------------|---------------------------|---|--|----------------------|
| Donkinsbaai             | Trigonephrus            | bonaespei                                 |                          |                            |                           | W. (C.)                                       |  |                      |
| 31.54S 18.17E           |                         |   |                          |                            |                           |   |  |                      |
| 05/06/95                | 35 71%                  | 22 65.7%                                  |                          |                            |                           | 2 5.7%  |  | 1 2.9%               |
| Lamberts Bay            | Trigonephrus            | bonaespei                                 |                          |                            |                           | W. (C.) sp. A                                 |  |                      |
| 32.05S 18.19E           |                         |   |                          |                            |                           |   |  |                      |
| 05/06/93                | 9 55.6%                 | 3 33.3%                                   |                          |                            |                           | 2 22.2%                                       |  |                      |
| Lamberts Bay            | Theba pisana            |   |                          |                            |                           |   |  |                      |
| 32.05S 18.19E           |                         |   |                          |                            |                           |   |  |                      |
| 05/06/93                | 106 17.9%               | 5 4.7%                                    |                          |                            |                           |   |  | 13 12.3%             |
| Elands Bay              | Theba pisana            | bonaespei                                 |                          |                            |                           |   |  |                      |
| 32.19S 18.20E           |                         |   |                          |                            |                           |   |  |                      |
| 05/06/109               | 147 21.1%               | 4 2.7%                                    |                          |                            |                           | 1 0.7%  |  | 26 17.7%             |
| Roscherpan Nat. Res.    | Trigonephrus            | bonaespei                                 |                          |                            |                           |   |  |                      |
| 32.36S 18.18E           |                         |   |                          |                            |                           |   |  |                      |
| Feurer & Theell         |                         | 4 ♀♀, 1 ♂                                 |                          |                            |                           |   |  |                      |
| Yzerfontein             | Theba pisana            | bonaespei                                 |                          |                            |                           | ?   |  |                      |
| 33.20S 18.10E           |                         | obibensis                                 |                          |                            |                           |   |  |                      |
| DW, GT & GM Gess        |                         | namaqua                                   |                          |                            |                           |   |  |                      |
|                         | 200 9.5%                | 6 3%                                      |                          |                            |                           | 1 0.5%  |  | 12 6%                |
| Yzerfontein             | Theba pisana            |   |                          |                            |                           | ?   |  |                      |
| 33.20S 18.10E           |                         |   |                          |                            |                           |   |  |                      |
| 06/07/14                | 256 16.8%               | 12 4.6%                                   |                          |                            |                           | 3 1.17%                                       |  | 28 10.94%            |
| Melkbosstrand           | Theba pisana            | bonaespei                                 |                          |                            |                           |   |  |                      |
| 33.42S 18.26E           |                         |   |                          |                            |                           |   |  |                      |
| 05/06/119               | 155 20.6%               | 7 4.5%                                    |                          |                            |                           |   |  | 23 14.8%             |
| Melkbosstrand           | Helix aspersa           |   |                          |                            |                           |   |  |                      |
| 33.42S 18.26E           |                         |   |                          |                            |                           |   |  |                      |
| 05/06/119               | 1                       | 1   |                          |                            |                           |   |  |                      |
| N Bloubergstrand        | Trigonephrus            | bonaespei                                 |                          |                            |                           |   |  |                      |
| 33.46S 18.27E           |                         |   |                          |                            |                           |   |  |                      |
| 05/06/110+112           | 7 57.1%                 | 3 43%                                     |                          |                            |                           |   |  | 1 14.3%              |
| N Bloubergstrand        | Theba pisana            |   |                          |                            |                           |   |  |                      |
| 33.46S 18.27E           |                         |   |                          |                            |                           |   |  |                      |
| 05/06/110               | 130 23.8%               | 12 9.2%                                   |                          |                            |                           | 9 6.9%  |  | 12 9.2%              |
| N Bloubergstrand        | Theba pisana            | bonaespei                                 |                          |                            |                           |   |  |                      |
| 33.46S 18.27E           |                         |   |                          |                            |                           |   |  |                      |
| 05/06/112               | 134 11.9%               | 3 2.2%                                    |                          |                            |                           |   |  | 13 9.7%              |

Appendix. Continued.

| Site<br>collection no.                | Shell ID<br>no & % used | Masarinæ nesting<br>in sand-filled shells | Chrysidiidae<br>"parasites" | Bombyliidae<br>"parasites" | Mutillidae<br>"parasites" | Megachilidae nesting in<br>empty snail shells | Eumeninae nesting in<br>empty snail shells | Spiders<br>residents |
|---------------------------------------|-------------------------|---|-----------------------------|----------------------------|---------------------------|---|--|----------------------|
| Bloubergstrand<br>33.46S 18.27E       | Helix aspersa           |   |                             |                            |                           |   |  |                      |
| 05/06/112                             | 3                       |   |                             |                            |                           |   |  |                      |
| Bloubergstrand<br>33.46S 18.27E       | Theba pisana            |   |                             |                            |                           |   |  |                      |
| 02/03/99                              | 25 32%                  | 2 8%                                      |                             |                            |                           | W. (C.) e.                                    |  | 6 24%                |
| Still Bay<br>34.22S 21.27E            | Theba pisana            |   |                             |                            |                           |   |  |                      |
| 02/03/104                             | 388 6.7%                |   |                             |                            |                           |   |  |                      |
| Witsand<br>34.23S 20.52E              | Theba pisana            | australis                                 |                             |                            |                           | 5 1.3%  |  | 20 5.2%              |
| 02/03/101                             | 69 48%                  | 16 23.2%                                  |                             |                            |                           | ? W. (C.)                                     |  | 17 24.6%             |
| Wilderness<br>34.00S 22.39E           | Theba pisana            |   |                             |                            |                           |   |  |                      |
| 02/03/103                             | 85 26%                  |   |                             |                            |                           | 3 3.5%  |  | 15 21.7%             |
| Maitland River Mouth<br>33.59S 25.17E | Tropidophora ligata     |   |                             |                            |                           |   |  | 10 3.94%             |
| 06/07/16                              | 254 3.94%               |   |                             |                            |                           |   |  |                      |
|                                       | Theba pisana 3 0%       |   |                             |                            |                           |   |  |                      |
|                                       | Achatina 3 0%           |   |                             |                            |                           |   |  |                      |
|                                       | Theba pisana            |   |                             |                            |                           |   |  |                      |
| Sardinia Bay<br>34.02S 25.32E         |                         |   |                             |                            |                           |   |  |                      |
| 06/07/5                               | 337 5.34%               |   |                             |                            |                           | ?   |  |                      |
| Sardinia Bay<br>34.02S 25.32E         | Tropidophora<br>ligata  |   |                             |                            |                           | 1   |  | 17 5.04%             |
| 06/07/6                               | 202 1.49%               |   |                             |                            |                           |   |  |                      |
| Bluewater Bay<br>33.51S 25.38E        | Theba pisana            |   |                             |                            |                           |   |  | 3 1.49%              |
| 06/07/8                               | 200 0%                  |   |                             |                            |                           |   |  |                      |
| Bluewater Bay<br>33.51S 25.38E        | Tropidophora<br>ligata  |   |                             |                            |                           |   |  |                      |
| 06/07/8                               | 300 0%                  |   |                             |                            |                           |   |  |                      |
| Boknes<br>33.45S 26.35E               | Tropidophora            |   |                             |                            |                           |   |  |                      |
| 06/07/9                               | 100 0%                  |   |                             |                            |                           |   |  |                      |
| Boknes<br>33.45S 26.35E               | Tropidophora<br>ligata  |   |                             |                            |                           |   |  |                      |
| 06/07/10                              | 380 1.58%               |   |                             |                            |                           |   |  | 6 1.58%              |

Appendix. Continued.

| Site<br>collectors' no.  | Shell ID<br>no & % used      | Masarinae nesting<br>in sand-filled shells | Chrysididae<br>"parasites" | Bombyliidae<br>"parasites" | Mutillidae<br>"parasites" | Megachilidae nesting in<br>empty snail shells | Eumeninae nesting in<br>empty snail shells | Spiders<br>residents |
|--|------------------------------|--|----------------------------|----------------------------|---------------------------|---|--|----------------------|
| Kenton-on-Sea<br>33.42S 26.40E   | Tropidophora ligata          |  |                            |                            |                           | Remains of bee nest                           |  |                      |
| 06/07/1  | 100 5%                       |  |                            |                            |                           | 2 2%  |  |                      |
| Kenton-on-Sea<br>33.42S 26.40E   | Tropidophora ligata          |  |                            |                            |                           | Remains of bee nests<br>and bees              |  |                      |
| 06/07/2  | 106 17.9%                    |  |                            |                            |                           | W (C.) ?e.<br>13 12.3%                        |  | 5 4.7%               |
| Port Alfred<br>E. Mc C. Callan<br>1979 in Gess and Gess<br>1988        | Tropidophora ligata          |  |                            |                            |                           | W. (C.) e.<br><br>5 emerged                   |  |                      |
| Port Alfred, Salt Vlei,<br>habitat destroyed by<br>housing development | Tropidophora ligata,<br>4 0% |  |                            |                            |                           |   |  |                      |
| 33.37S 26.53E  | Helix aspersa                |  |                            |                            |                           |   |  |                      |
| 06/07/4  | 2 0%                         |  |                            |                            |                           |   |  |                      |
| Riet River Mouth<br>33.34S 27.01E                                      | Tropidophora ligata          |  |                            |                            |                           | W (C.) ?e.                                    |  |                      |
| 06/07/3  | 41 7.3%                      |  |                            |                            |                           | 2 4.9%  |  |                      |
| Riet River Mouth<br>33.34S 27.01E                                      | Theba pisana                 |  |                            |                            |                           |   |  |                      |
| Kaltenpoth   | 300 4%                       |  |                            |                            |                           | 3 1%  |  | 9 3%                 |

## Nest Structure, Seasonality, and Host Plants of *Thygater aethiops* (Hymenoptera: Apidae, Eucerini) in the Andes

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**Abstract.**—*Thygater* is a Neotropical genus of 30 species of solitary bees occurring from Mexico to Argentina. Information on the nesting biology is only available for a single species, *T. analis*, from southern Brazil. We studied the nest architecture, seasonality, and host plants of *T. aethiops* in two localities in the Eastern Andes of Colombia (~ 2700–2900 m). Bees nested singly or forming aggregations in flat ground or sloping surfaces. Nests were deep (39–59 cm) and consisted of an unlined but smooth long main tunnel meandering downward from the surface. Nests had three to seven nearly vertical cells, which were located singly at the ends of short vertical tunnels that descended from the main tunnel. The older brood was located closer to the nest entrance, indicating a progressive nest development. Monthly sampling and appraisal of museum specimens showed that, although females were more commonly collected than males, both sexes were present year-round. We present a list of 32 plant species (27 genera in 18 families), including exotic, native, and cultivated plants used by *T. aethiops* in Colombia. The most noticeable differences from *T. analis* are in the pattern of nest development and seasonality. *Thygater aethiops* builds nests in a progressive manner and it is likely to be multivoltine, whereas *T. analis* has a regressive nest development (i.e., older brood located far from the entrance) and a single generation per year. Long-term studies on different populations are required to determine if *T. aethiops* has continuous brood production or if larval diapause occurs at some point during the year.

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The purpose of this paper is to provide information on the nest architecture, seasonality and host plants of *Thygater aethiops* (Smith) at higher elevations in the Colombian Andes. *Thygater* Holmberg is a Neotropical genus of 30 species of solitary bees occurring from Mexico to Argentina (Urban 1967, 1999). The biology of *Thygater* is still poorly known. Information on the nesting biology is only available for a single species, *T. analis* (Lepeletier), from southern Brazil (Michener and Lange 1958, Rozen 1974). *Thygater aethiops* is widely distributed in the Neotropical region, occurring from Costa Rica to Argentina, and is largely sympatric with *T. analis* in most of its range (Urban 1967). In Colombia, *T. aethiops* is found between 1400 and 3500 m of elevation and is the most

common species of the genus. Nests of this species are frequently found in grazing pastures, city parks, gardens, and along sidewalks in towns and densely populated cities such as Bogotá (Gonzalez and Engel 2004, Gonzalez et al. 2005).

We studied the nesting biology of *T. aethiops* in two localities in the Eastern Andes of Colombia (~ 2700–2900 m), and compared it with that of *T. analis*. We describe the nest and, based on monthly samplings and examination of museum specimens, we show that both sexes of *T. aethiops* are present year-round, visiting flowers of exotic, native, and cultivated plants. The nesting biologies of both species are very similar, except for the pattern of nest development and seasonality. *Thygater aethiops* builds nests in a



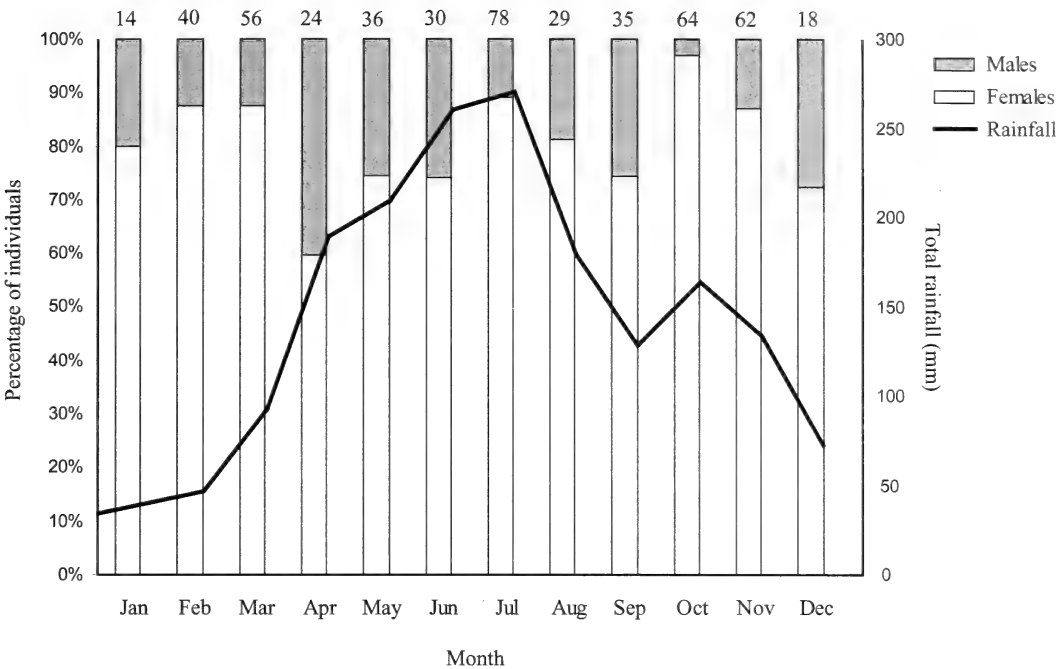


Fig. 1. Seasonal collections of *Thygater aethiops* at high altitudes (2700–2900 m) in the Andes of Colombia. Monthly surveys were done in 1999 in La Calera (Departamento of Cundinamarca), except in January, April, May, June and December. To complete the seasonal cycle, we used the number of museum specimens collected in La Calera and contiguous areas during those months. Females were more commonly collected than males ( $X^2_{.001\ [22]} = 534.1, P < 0.001$ ) every month, and the female/male ratios were not homogeneous among months ( $X^2_{.05\ [11]} = 28.9, P < 0.001$ ). The total number of individuals is indicated at the top of each column.

progressive manner (i.e., older brood located near the entrance, thus first to be completed), and is likely to be multivoltine, whereas *T. analis* has regressive nest development and a single generation per year. However, long-term studies on different populations are required to determine if *T. aethiops* has continuous brood production or if larval diapause occurs at some point during the year, and to detect any variation in nest development depending on soil conditions.

MATERIAL AND METHODS

Study sites and nest excavations

The nesting biology of *T. aethiops* was studied by VG during December 2004 in Mondoñedo (2720 m, 4°39'52.9"N, 74°17'2"W), whereas the seasonality and host plants were studied in 1999 by MO in La Calera (2900 m, 4°43'22"N, 73°58'18"W).

Mondoñedo is a semiarid area highly disturbed by cattle ranching, gravel extraction, and waste dumping whose soils are very compacted, shallow, and strongly eroded (details in Gonzalez and Chávez 2004). The soils in La Calera are looser and less eroded than in Mondoñedo, and primarily used to grow potato, corn, beans, and wheat (IGAC 1996). Annual rainfall in La Calera is bimodal (Fig. 1), with higher monthly precipitation than in Mondoñedo.

We excavated the nests using a geological pick, hand shovel, wood chisels and a pocketknife. Prior to excavation, and in order to trace the nest structure, we used a syringe to inject into the tunnel a slurry of plaster-of-Paris and water, which was allowed to harden for about 2–5 minutes; we then excavated the nests. We measured nest features in the field using a caliper. Maximum nest depth was measured from the nest entrance to the bottom of the deepest cell.

Seasonality

We collected bees on flowers and examined museum specimens to determine the seasonal cycle of *T. aethiops* in La Calera. Bees were collected when they appeared to be more active, frequently between 8:00 and 11:00 am, and from one to three days each month depending on weather conditions. Once we identified and sexed them, bees were released. *Thygater aethiops* is the only species of the genus occurring in La Calera. However, we decided to capture them because sometimes it was difficult for us to distinguish *T. aethiops* females from small, black workers of the bumble bee *Bombus atratus* Franklin (Apidae, Bombini). Males and females of *T. aethiops* were easy to distinguish in the field because, as in other eucerines, males have longer antennae that surpass the base of the abdomen.

The monthly surveys in La Calera were done during the year of 1999, except in January, April, May, June, and December. To complete the seasonal cycle, we used the number of museum specimens collected in La Calera and contiguous areas during those months. We used a G-test (Sokal and Rohlf 2000) to compare percentages of males and females of *T. aethiops*, and to determine if female/male (F/M) ratios were homogeneous among months.

Host plants

We recorded the plants visited by *T. aethiops* in La Calera, and also extracted floral records from data from specimen labels. We examined about 300 specimens of *T. aethiops* deposited in the Snow Entomological Museum, University of Kansas, USA (SEM), National Museum of Natural History, Washington, D.C. (USNM), and the following Colombian institutions: Laboratorio de Investigaciones en Abejas, Departamento de Biología (LABUN), and the Museo de Historia Natural, Instituto de Ciencias Naturales (ICN) in Bogotá, Instituto de Investigación de Recursos Biológicos Alexander von Hum-

Table 1. Measurements (cm) of some structures of eight nests of *Thygater aethiops*.  $\bar{x}$ : mean value,  $\pm$ : standard error, R: range, N: sample size. Samples varied in number because, to increase variation, we measured remains of nest structures (e.g., cells, tunnels) that we found during excavations.

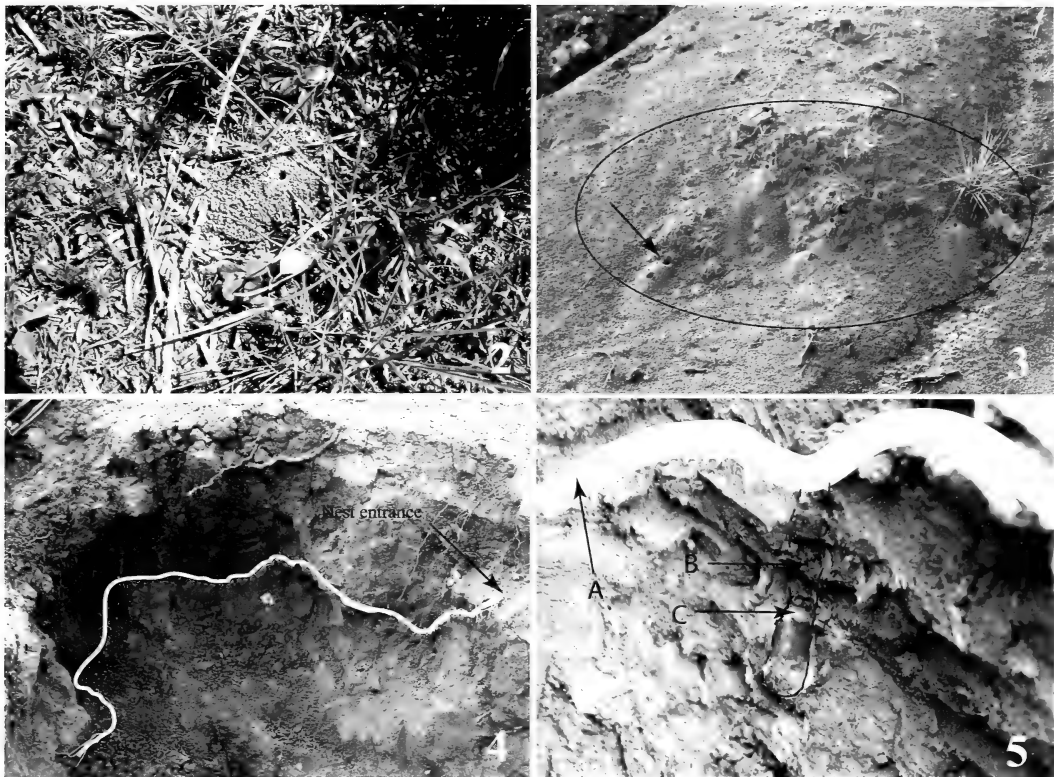
| Nest structure                            | $\bar{x} \pm$  | R         | N  |
|---|----------------|-----------|----|
| <b>Nest density (nests/m<sup>2</sup>)</b> | 3.3 $\pm$ 0.6  | 1.0–4.4   | 6  |
| <b>Inter-nest distance</b>                | 27.5 $\pm$ 7.5 | 4.0–108   | 13 |
| <b>Maximum nest depth</b>                 | 43.8 $\pm$ 3.1 | 36–59     | 4  |
| <b>Tumulus</b>                            |                |           |    |
| Length                                    | 8.3 $\pm$ 1.0  | 6.0–10    | 4  |
| Width                                     | 9.3 $\pm$ 0.9  | 8.0–12    | 4  |
| <b>Nest entrance</b>                      | 0.75 $\pm$ 0.1 | 0.68–0.80 | 17 |
| <b>Main tunnel</b>                        |                |           |    |
| Length                                    | 64 $\pm$ 10    | 53–94     | 4  |
| Diameter                                  | 0.85 $\pm$ 0.1 | 0.80–0.93 | 16 |
| <b>Laterals</b>                           |                |           |    |
| Length                                    | 2.20 $\pm$ 0.2 | 1.08–3.30 | 13 |
| Diameter                                  | 0.76 $\pm$ 0.2 | 0.67–0.80 | 6  |
| <b>Cell depth</b>                         | 36 $\pm$ 2.6   | 21–59     | 18 |
| <b>Number of cells per nest</b>           | 5.0 $\pm$ 0.7  | 3–7       | 8  |
| <b>Cell dimensions</b>                    |                |           |    |
| Length                                    | 1.89 $\pm$ 0.6 | 1.8–2.0   | 5  |
| Diameter                                  | 0.88 $\pm$ 0.2 | 0.83–0.95 | 5  |

boldt (IAvH), Villa de Leyva, Boyacá, and the Museo Entomológico Francisco Luis Gallego, Universidad Nacional de Colombia in Medellín (MEFLG).

RESULTS

Nest architecture

Nest measurements are given in Table 1. Nests were found singly or forming aggregations in flat ground or sloping surfaces. The nest sites were either barren or sparsely covered with grasses in areas frequently well exposed to the sun (Figs 2, 3). Nest entrances were circular and when nests were active, irregular tumuli extended downward from the nest entrances. Nests were deep, and consisted of an unlined but smooth long main tunnel meandering downward from the surface (Fig. 4). Cells were nearly vertical and placed singly at the ends of short laterals, or vertical tunnels that descended from the main tunnel. Once the cells were completed, these vertical tunnels were filled with loose, coarse soil (Fig. 5).



Figs 2–5. Nests of *Thygater aethiops*. 2, single nest in flat ground; note the tumulus around nest entrance. 3, cluster of nests in a barren, sloping surface; all nest entrances are encircled and one of them is indicated by an arrow. 4, an excavated nest showing the meandering main tunnel, indicated by a white solid line. 5, detailed view of a cell in sagittal section; A, main tunnel; B, short laterals filled with loose soil after cell completion; C, whitish spiderweb-like layer, likely a mass of mold hyphae, found in most of excavated cells (nest measurements in Table 1).

The cells were excavated in the soil and were not separable from the substrate. The three to seven cells per nest were constructed at different depths. The cells were elongated, with a concave spiral closure inside, slightly wider at the bottom than top, and lined with a “wax-like” secreted material resembling those of other eucerine bees. In most cells, the upper one third of the inner wall was covered with a thin, whitish spiderweb-like layer (Fig. 5). We did not examine it under the microscope, but it might be a mass of mold hyphae. As described for *Thygater* (Rozen 1974, Packer 1987), larval feces were incorporated within the dark brown, paper-like cocoon. The basal one third of the cell contained liquid provisions with the egg floating on the surface. Cell contents ranged from eggs to

small larvae and pollen. Older brood was located closer to the nest entrance, indicating progressive nest development. Numerous old burrows and remains of cocoons from older generations were commonly found during excavations.

Associated organisms

We found empty puparia of an unknown fly inside three sealed cells that had a perforation (2.0–2.6 mm in diameter) in the cell closure. Each cell had from two to six puparia, about 3.8 mm long and 1.5 mm wide, among debris.

Seasonal cycle

The monthly sampling in La Calera and appraisal of museum specimens revealed that both sexes are present on every month

of the year (Fig. 1). Moreover, females were more commonly collected than males ( $X^2_{.001 [22]} = 534.1$ ,  $P < 0.001$ ), and the F/M ratios were not homogeneous among months ( $X^2_{.05 [11]} = 28.9$ ,  $P < 0.001$ ). F/M ranged from about 2:1 in January to 31:1 in October (Fig. 1).

### Host plants

Both males and females were recorded from 32 plants species (27 genera in 18 families), including exotic, native, and cultivated plants. Females were recorded from the most plants. Records for males are indicated with an asterisk. AGAPANTHACEAE: *Crinum africanum* L'Héritier de Bruttelle\*. ASTERACEAE: *Baccharis* sp., *Senecio* sp., *Vernonia canescens* Kunth. BALSAMINACEAE: *Impatiens balsamina* Linnaeus. BRASSICACEAE: *Brassica napus* Linnaeus\*, *B. nigra* (Linnaeus)\*, *Raphanus raphanistrum* Linnaeus\*. CAESALPINACEAE: *Cassia tomentosa* Linnaeus. CONVULVACEAE: *Convolvulus* sp., *Ipomoea congesta* R. Br. CUCURBITACEAE: *Cyclanthera pedata* Scrad, *Sechium edule* Swartz. FABACEAE: *Desmodium uncinatum* (Jacquin), *Phaseolus vulgaris* Linnaeus\*, *Trifolium pratense* Linnaeus\*, *T. repens* Linnaeus\*. LAMIACEAE: *Salvia cuatrecasana* Epling\*, *S. bogotensis* Benth\*. MALVACEAE: *Hibiscus grandiflorus* Juss. Ex Candolle. MELASTOMATACEAE: *Tibouchina* sp. PAPAVERACEAE: *Papaver somniferum* Linnaeus\*. PASSIFLORACEAE: *Passiflora mollissima* L.H. Bailey. ROSACEAE: *Rubus* sp\*. RUBIACEAE: *Coffea arabica* Benth, *Palicourea* sp. RUTACEAE: *Citrus aurantium* Linnaeus. SOLANACEAE: *Cyphomandra betacea* (Cav.) Sendtn, *Solanum tuberosum* Poepp ex Walp\*, *S. lycioides* Linnaeus. *Solanum* sp. TROPAEOLACEAE: *Tropaeolum majus* Linnaeus\*.

### DISCUSSION

The nest architecture of *T. aethiops* is very similar to that described for *T. analis*, the only species of *Thygater* whose nests have been studied (Michener and Lange 1958, Rozen 1974). Both species nest solitarily or in aggregations in flat or sloping ground.

Their nests consist of a long, unlined, main tunnel from which short laterals, ending in a single vertical elongated cell, branch off; these laterals are filled with soil once cells are completed. The most noticeable difference from *T. analis* is the pattern of nest development. We inferred from the distribution of young and old brood in the excavated nests, that *T. aethiops* builds nests in a progressive manner (i.e., older brood located near the entrance, thus, first to be completed) whereas it is regressive in *T. analis* (older brood located far from the entrance). However, we examined nests of *T. aethiops* from a single population and only during the dry season, so we do not know if the nest development pattern varies among localities, with time of year, or with soil hardness.

The monthly surveys in La Calera and the appraisal of museum specimens showed that males and females are present throughout the year. In La Calera, females were more frequently collected than males, and the F/M ratios varied significantly among months (Fig. 1). We did not determine adult longevity but unless adults have an extraordinary long life, the presence of both sexes indicates that *T. aethiops* must be multivoltine. In contrast, due to seasonality in southern Brazil, *T. analis* over-winters as postdefecating larvae and emerge as adults during the summer. *Thygater analis* is the most widespread species of the genus, occurring from tropical to subtropical lowlands to high altitudes in the Andes (Urban 1967) and thus could have multiple generations per year in more tropical environments as does *T. aethiops*. However, we do not know if *T. aethiops* has continuous brood production or if larval diapause occurs at some point during the year, as it has been observed in other Andean solitary bees, such as *Anthophora walteri* Gonzalez (Apidae, Anthophorini) (Gonzalez and Chávez 2004).

*Thygater aethiops* seems to use a wide range of exotic, native, and cultivated plants for pollen and nectar (e.g., *Impatiens*,

*Salvia* spp. and *Solanum tuberosum*, respectively). Our records agree with the apparent polylectic diet of *Thygater*, as inferred by Urban (1967) based on scarce floral records. Also, as previously noted for some *Thygater* species (Urban 1967), females of *T. aethiops* buzz pollinate flowers with poricidal anthers (e.g., *Solanum*). It might be interesting to explore the use of *T. aethiops* as a crop pollinator of tomatoes (*Solanum lycopersicum* Linnaeus) or Inca berries (*Physalis peruviana* Linnaeus), both Solanaceae species with poricidal anthers that are extensively cultivated in the Andean region. Undoubtedly, research on adult longevity, brood production, and other biological aspects of *T. aethiops* are needed.

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## A Comparison of the Parasitic Wasps (Hymenoptera) at Elevated Versus Ground Yellow Pan Traps in a Beech-Maple Forest

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*Abstract.*—The abundance, diversity, and morphospecies composition of the parasitic wasp fauna is compared at two levels in an Ohio (USA) temperate forest. The ground layer and the elevated layer (~10m) exhibited similar abundance but a distinctly different composition. The diversity at the ground layer was greater. Encyrtidae were captured more often in elevated traps while Pteromalidae, Ichneumonidae, and alysiine Braconidae were more prevalent at ground level. A retrospective analysis of the edge effect showed no difference in the composition relative to distance from forest edge but elevated samples had a higher diversity near the edge than in the interior.

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A key goal in ecology is to describe the distribution of species within the environment. However, difficulty of canopy access has limited our knowledge of forest communities (Ozanne et al. 2003). A better understanding of arthropod forest stratification is needed to identify which taxa are dependent on elevated strata and under what conditions do distinct stratum communities develop. This will direct more efficient and thorough surveys of forest life.

There are many accounts of arthropod stratification in tropical forests. Many document increased abundance (e.g. Kato et al. 1995, Barrios 2003, Sutton and Hudson 1980) and diversity (e.g. Basset 2001a, Basset et al. 2001, Rees 1983, Yanouvier and Kaspari 2000) in elevated layers. Contradictory results however are evident. For example, Stork and Grimbacher (2006) found a similar abundance and richness of beetles between ground and elevated layers. Abundant arthropod stratum specialists have also been observed (Schulze et al. 2001, Hammond et al. 1997, Sorensen 2003).

Temperate forests are also stratified but patterns are similarly not well established. The stratum of peak abundance has been

shown to be variable: elevated (Hollier and Belshaw 1993); near ground (Nielsen 1987), or comparable (Le Corff and Marquis 1999, Preisser et al. 1998, Ulyshen and Hanula 2007). In several studies diversity has been shown to be greater near ground level (Lowman et al. 1993, Le Corff and Marquis 1999, Ulyshen and Hanula 2007). Distinct stratum communities were revealed in the preceding and by Winchester and Ring (1996), Gibson (1947) and Hollier and Belshaw (1993). But Fowler (1985) observed little stratification in richness or species composition of herbivores on birch branches. Examples of stratification involving a limited number of species include Munster-Swendsen (1980) and Henry and Adkins (1975).

Although there has been pronounced growth in canopy research in recent decades (Basset 2001b), basic questions regarding forest stratification remain. I am not aware of another temperate zone species-level survey that addresses the complete parasitic wasp fauna at ground versus elevated strata. The purpose of this study is to compare the composition of adult parasitic wasps at two levels of a temperate forest.

## METHODS

The study site is located within the Soubusta Sugarbush Preserve (041°34'24" N 081°14'04" W) in northeastern Ohio, USA. Canopy trees are dominated by sugar maple (*Acer saccharum* Marshall) and American beech (*Fagus grandifolia* Ehrh.). Tulip tree (*Liriodendron tulipifera* L.) is also common. Ground cover is dominated by sugar maple seedlings, mayapple (*Podophyllum peltatum* L.), white trillium (*Trillium grandiflorum* Salisb.), and white ash (*Fraxinus americana* L.) seedlings. The site was deforested in the 19<sup>th</sup> century and has been harvested for maple syrup since the 1940s but apparently no tree thinning has been practiced (K. Vouk, pers. comm.). The study site is within a forested lot which is approximately 85 hectares and connected to other lots by a corridor.

Traps were made from plastic containers spray-painted fluorescent yellow. The dimensions (L-W-D) were 20×15×10 cm. A bow and arrow were used to string a line for eight traps hung over sugar maple limbs. Trap placement was dictated by the presence of an accessible tree limb under the closed canopy. Elevated trap placement ranged from 6.7 to 11.9 meters (mean 9.8 m) high. A ground level trap was placed directly under each elevated trap. Rope was attached to the trap and fastened to a nearby tree to mimic the elevated trap set-up. All traps were filled half way with water and a few drops of unscented detergent.

Traps were serviced every two days from June 3<sup>rd</sup> to July 1<sup>st</sup> 2005. Specimens of parasitic wasps (including all Cynipoidea; excluding Dryinidae) were pointed and sorted to morphospecies. Occasionally, within a single pan sample, only representative specimens of a common morphospecies were pointed. Inherent in the concept of morphospecies is the likelihood of misclassification. Approximately 60 hours were spent sorting specimens in an effort to minimize this occurrence. Seventeen

specimens are unassigned to morphospecies owing to damage or uncertainties regarding sexual dimorphism. Specimens were taken at least to family level using Goulet and Huber (1993). Braconid specimens were taken to subfamily using Wharton et al. (1997). Representative specimens are housed at the Cleveland Museum of Natural History.

Paired *t* tests were used to compare various components of each stratum. The Mann-Whitney Rank Sum Test was used when the data were not normally distributed. The Simpson Index of diversity was used as recommended by Magurran (2004). The Morisita-Horn index was used to measure the faunal similarity between groups. It uses abundance data and is preferable because it is not dependent on sample size (Krebs 1999).

All traps were within 250 meters of each other. Two pairs of traps (sites #1 and #2) were placed approximately 25 m from an old field while the remaining were situated 100 ± 10 meters from the forest edge. Although this set-up was not designed to address any edge effects, a retrospective comparison of these two groups was carried out. To examine the faunal composition of the sites, a cluster analysis using MVSP version 3.130 (Kovach 2005), the UPGMA clustering method, and the modified Morisita's coefficient of similarity was executed. Also, the Morisita-Horn index was compiled for each pair of traps per stratum. Trap pairs sited a similar distance from the edge were compared with those sites at differing distances by means of a *t* test.

## RESULTS

A total of 2,541 specimens and 269 morphospecies were collected. The braconid, *Eubazus pallipes* Nees, represents 36.4 % of the total catch. Ninety-five percent of the specimens (878 specimens) were from a single elevated trap taken during five consecutive collecting dates. Therefore, *E. pallipes* is not included in the following

Table 1. Abundance and diversity of each stratum.

|                    | Abundance                            | Number of species                    | Simpson index (1/D)                      |
|--------------------|--------------------------------------|--------------------------------------|--|
| Elevated *         | 703                                  | 147                                  | 20.18                                    |
| Ground *           | 837                                  | 183                                  | 41.79                                    |
| Mean (SD) **       | elev. 6.38 (2.84)<br>gr. 7.61 (3.21) | elev. 4.92 (1.34)<br>gr. 6.35 (2.47) | elev. 0.915 (0.041)<br>gr. 0.941 (0.025) |
| t test (N = 30) ** | t = -1.114 P = 0.275                 | t = -1.964 P = 0.059                 | t = -2.164 P = 0.039                     |

\* data deleted to yield equal collection effort (216 trap days per stratum)  
\*\* based on raw data

analysis where it would skew the results. Traps were occasionally disturbed, resulting in unequal collection effort between the strata. This was corrected for by deleting the data from each pair of traps when one was disturbed in comparisons that do not use the mean.

The abundance of parasitic wasps was similar between strata (Table 1). The diversity was significantly higher at ground level based on the Simpson Index but marginally insignificant based on species richness (Table 1). Based on equal collection effort, there were 130 singletons: 54 from elevated traps and 76 at ground level. This does not represent a significant difference ( $t = -1.25$ ,  $P = 0.223$ ).

The inter-strata similarity is low, 0.353, compared to the mean (SD) of the within stratum similarity: elevated 0.708 (0.088),

ground 0.586 (0.084). Similarly, Figure 1 shows the composition of the strata were distinct. Table 2 lists the taxa with at least ten specimens. Six of the 14 families and 21 of the 45 morphospecies were significantly more abundant in a particular stratum. Excluding *Eubazus pallipes* (from the trap with the exceptional catch), the abundance of the 21 “stratum specialists” represented 67% of the “common morphospecies” listed in Table 2. This proportion rises to 71% if the morphospecies at  $P \leq 0.08$  are considered stratum specialists.

The influence of the edge effect on diversity is shown in Table 3. There was a significantly higher diversity in the elevated traps near the edge but no significant difference at ground level. Table 4 and Figure 1 show no edge effect in the species composition for either stratum.

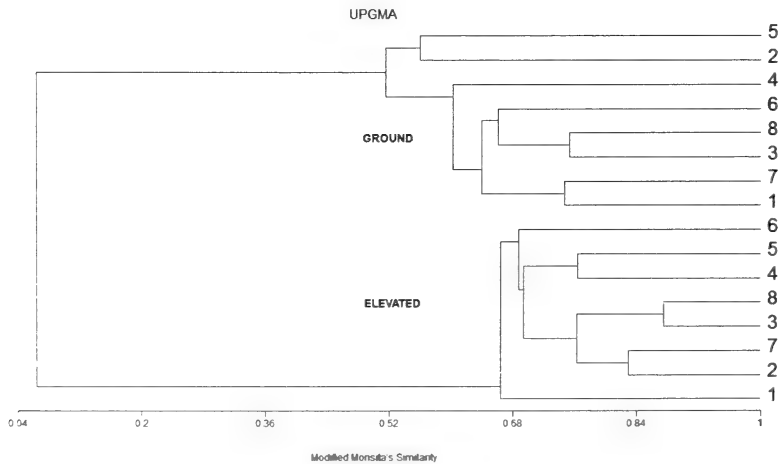


Fig. 1. Cluster analysis of the abundance based species composition for each trap. Sites one and two were approximately 25 meters from the forest edge while the remaining were approximately 100 meters away.



## DISCUSSION

The parasitic wasp fauna differed between strata at the family level (individuals per family) and the morphospecies level. Although elevated traps were in the lower reaches of the sugar maple canopy and the forest floor contained abundant sugar maple seedlings, numerous taxa were found in significantly higher numbers in the elevated traps. Likewise, some morphospecies exhibited a preference for the ground level. My results are consistent with Le Corff and Marquis (1999) and Ulyshen and Hanula (2007) who also found distinctly different insect communities at elevated and near ground strata in temperate habitats. Additionally, they also found the near ground stratum was more diverse.

These results are consistent with Lowman et al. (1993) who hypothesized that the stratum of peak diversity will generally be near the ground in temperate forests and in the canopy in tropical forests, coinciding with the stratum with the most niches. Further evidence includes Leksono et al. (2005) who used both yellow and blue pan traps to survey attelabid and cantharid (Coleoptera) stratification in a mixed deciduous forest in Japan. Although common species were more abundant at the highest (20m) layer, rare species were found only at the lower layers (0.5m and 10m). In contrast, the canopy is often shown to be more diverse in tropical forests (e.g. Basset 2001a, Rees 1983, Yanouvial and Kaspari 2000).

The particular sampling regime in this study precludes examination of the influence of some known factors that affect insect collections. Seasonality has been shown to influence guild structure (Askew and Shaw 1979, Sheehan 1994). Ulyshen and Hanula (2007) found the ground: canopy ratio of abundance and richness is liable to change significantly throughout the collecting season. Ozanne (1999) found guild structure changes with tree species.

Davis and Sutton (1998) found forest type influences the vertical distribution of certain dung beetles. Also, it is well known that collecting method influences the composition of parasitic wasp samples (Noyes 1989, Idris et al. 2001). Perhaps because yellow pan traps are attractive the focus on a single tree species is not necessary to collect comparable samples in the canopy but this has not been established.

The edge effect has been shown to change the species composition and increase the abundance of insects (e.g. Noyes 1989, Foggo et al. 2001). The lack of a decipherable edge community in this study could be due to the rather distant (25 m) location of the "edge" sites. Alternatively, the gradient may be much weaker. For example, Dangerfield et al. (2003) found habitat specialists can be prevalent for hundreds of meters beyond a discrete riparian/treeless saltbush edge. In this study, elevated edge sites displayed a greater diversity than the elevated interior sites but there was no significant difference at ground level. These results are preliminary due to the lack of replication of edge sites, but suggest that further work into the edge/canopy effect on parasitic wasps may be fruitful for building our knowledge of wasp biology and forest ecology.

The stratification displayed in Fig. 1 and Table 2 probably largely reflects host distribution. For example, alysiine braconids and the majority of diapriids attack immature Diptera which predominate in the soil layers of temperate forests (Schaefer 1991). Additionally, others have found certain groups of egg parasitoid abundance to be greater in elevated layers (Compton et al. 2000, Basset et al. 2001, Noyes 1989). Mymaridae however has been shown to be low fliers (Compton et al. 2000, Noyes 1989). Compton et al. (2000) demonstrated various chalcid families (esp. fig wasps) can be found above the canopy where there is stronger wind. A strong case is made that their presence at that height is associated with dispersal. Perhaps some parasitic

Table 2. List of taxa with at least ten specimens and a comparison of the vertical distribution.

| Taxa                            | Elevated Abundance<br>238 trap days | Ground Abundance<br>218 trap days | t test (t) or Mann-Whitney Rank Sum test (T) |
|---------------------------------|-------------------------------------|-----------------------------------|--|
| <b>Ceraphronoidea</b>           |                                     |                                   |  |
| <u>Ceraphronidae</u>            | 51                                  | 41                                | t = -0.305 P = 0.763                         |
| #1                              | 6                                   | 12                                | T = 269 P = 0.134                            |
| #2                              | 11                                  | 12                                | T = 249 P = 0.520                            |
| #3                              | 25                                  | 3                                 | T = 173 P = 0.015                            |
| <b>Chalcidoidea</b>             |                                     |                                   |  |
| <u>Encyrtidae</u>               | 146                                 | 27                                | t = -5.30 P = < 0.001                        |
| #1                              | 9                                   | 2                                 | T = 208 P = 0.316                            |
| #2                              | 22                                  | 7                                 | T = 199 P = 0.170                            |
| #3                              | 10                                  | 8                                 | T = 238 P = 0.835                            |
| #4                              | 33                                  | 0                                 | T = 158 P = 0.002                            |
| #5                              | 28                                  | 0                                 | T = 150 P = < 0.001                          |
| #6                              | 22                                  | 1                                 | T = 177 P = 0.021                            |
| <u>Eulophidae</u>               | 39                                  | 19                                | t = -1.75 P = 0.092                          |
| #1                              | 11                                  | 0                                 | T = 173 P = 0.130                            |
| #2                              | 1                                   | 9                                 | T = 280 P = 0.05                             |
| #3                              | 10                                  | 1                                 | T = 202 P = 0.202                            |
| <u>Mymaridae</u>                | 138                                 | 79                                | T = 209 P = 0.330                            |
| <i>Stephanodes</i> sp.          | 7                                   | 23                                | T = 287 P = 0.025                            |
| #1                              | 121                                 | 31                                | t = -2.98 P = 0.006                          |
| #2                              | 9                                   | 6                                 | T = 220 P = 0.602                            |
| <u>Pteromalidae</u>             | 15                                  | 36                                | t = 2.35 P = 0.026                           |
| #1                              | 1                                   | 18                                | T = 281 P = 0.047                            |
| <b>Cynipoidea</b>               |                                     |                                   |  |
| <u>Charipidae</u>               | 12                                  | 2                                 | T = 208 P = 0.316                            |
| #1                              | 11                                  | 2                                 | T = 208 P = 0.316                            |
| <u>Cynipidae</u>                | 14                                  | 31                                | T = 275 P = 0.081                            |
| #1                              | 8                                   | 22                                | T = 259 P = 0.288                            |
| <u>Eucoilidae</u>               | 1                                   | 9                                 | T = 288 P = 0.022                            |
| <b>Evanioidea</b>               |                                     |                                   |  |
| <u>Aulacidae</u>                | 10                                  | 0                                 | T = 188 P = 0.063                            |
| <b>Ichneumonoidea</b>           |                                     |                                   |  |
| <u>Braconidae</u>               | 984                                 | 113                               | T = 232 P = 0.983                            |
| <u>Alysiinae</u>                | 7                                   | 68                                | T = 326 P = < 0.001                          |
| <i>Aphaereta pallipes</i> (Say) | 1                                   | 9                                 | T = 272 P = 0.103                            |
| <i>Dinotrema</i> sp.            | 3                                   | 17                                | T = 276 P = 0.073                            |
| <u>Aphidiinae</u>               | 20                                  | 7                                 | T = 214 P = 0.441                            |
| <i>Trioxys</i> sp.              | 19                                  | 6                                 | T = 214 P = 0.453                            |
| <u>Doryctinae</u>               | 14                                  | 31                                | T = 277 P = 0.071                            |
| <i>Spathius elegans</i> Matt.   | 4                                   | 29                                | T = 303 P = 0.004                            |
| <u>Euphorinae</u>               | 8                                   | 2                                 | T = 202 P = 0.203                            |
| <u>Helconinae</u>               | 927                                 | 1                                 | T = 154 P = 0.001                            |
| <i>Eubazus pallipes</i> Nees    | 924                                 | 1                                 | T = 169 P = 0.009                            |
| <u>Ichneumonidae</u>            | 45                                  | 131                               | T = 321 P = < 0.001                          |
| #1                              | 1                                   | 9                                 | T = 257 P = 0.315                            |
| #2                              | 2                                   | 13                                | T = 255 P = 0.357                            |
| #3                              | 0                                   | 13                                | T = 293 P = 0.013                            |
| #4                              | 3                                   | 15                                | T = 272 P = 0.109                            |
| #5                              | 2                                   | 12                                | T = 275 P = 0.080                            |
| <b>Platygastroidea</b>          |                                     |                                   |  |
| <u>Platygastridae</u>           | 158                                 | 97                                | T = 216 P = 0.507                            |
| #1                              | 104                                 | 24                                | T = 172 P = 0.012                            |
| #2                              | 8                                   | 6                                 | T = 240 P = 0.787                            |
| #3                              | 4                                   | 7                                 | T = 241 P = 0.738                            |

Table 2. Continued.

| Taxa            | Elevated Abundance<br>238 trap days | Ground Abundance<br>218 trap days | t test (t) or Mann-Whitney Rank Sum test (T) |
|-----------------|-------------------------------------|-----------------------------------|--|
| #4              | 7                                   | 13                                | T = 263 P = 0.219                            |
| #5              | 12                                  | 13                                | T = 233 P = 1.0                              |
| #6              | 2                                   | 10                                | T = 275 P = 0.080                            |
| #7              | 3                                   | 17                                | T = 299 P = 0.006                            |
| Scelionidae     | 40                                  | 8                                 | T = 164 P = 0.004                            |
| Telenomus sp.   | 20                                  | 3                                 | T = 171 P = 0.010                            |
| Trissolcus sp.  | 11                                  | 0                                 | T = 195 P = 0.121                            |
| Proctotrupoidea |                                     |                                   |  |
| Diapriidae      | 22                                  | 244                               | T = 341 P = < 0.001                          |
| Basalys sp.     | 5                                   | 22                                | T = 293 P = 0.013                            |
| Paramesius sp.  | 0                                   | 17                                | T = 285 P = 0.030                            |
| Spilomicrus sp. | 1                                   | 10                                | T = 249 P = 0.502                            |
| Trichopria sp.  | 2                                   | 38                                | T = 326 P = < 0.001                          |
| #1              | 2                                   | 87                                | T = 335 P = < 0.001                          |
| #2              | 5                                   | 15                                | T = 283 P = 0.039                            |
| #3              | 0                                   | 11                                | T = 285 P = 0.030                            |
| #4              | 0                                   | 14                                | T = 300 P = 0.005                            |

wasps in temperate forests use elevated layers for dispersal. Evidence for this include Karem et al. (2006) who found the abundance of small wasps (many Chalcidoidea, Cynipoidea, and Proctotrupoidea) was similarly stratified along forest/field transects so that the wasps were flying in the canopy in addition to well above field vegetation. Nielsen (1987) found the greatest wind speeds just below the canopy (10m) in a fully leaved beech stand. Using light traps, it was shown that insects in general (including Hymenoptera) avoided this layer compared to traps at 0.6 m and 21 m. Unfortunately, the Hymenoptera composition per level was not documented.

Similar to my results, other studies that have compared canopy versus near ground

level insects have found approximately half of the common species to be associated with a particular stratum, about a quarter at each level (Stork and Grimbacher 2006, Broadhead 1983). Likewise, Ulyshen and Hanula (2007) report that the proportion of beetle species captured exclusively at a particular stratum to be approximately 30 % at each layer. Although most of the taxa with at least ten specimens are found at both strata in my study, it has been shown that the fauna collected at only one layer gives a biased representation of the composition of parasitic wasps.

Table 3. Edge effect and diversity for each stratum.

| Distance from edge | Simpson Index |               |           |
|--------------------|---------------|---------------|-----------|
|                    | N             | Mean (SD)     | t test    |
| Elevated           |               |               |           |
| ~25 m              | 2             | 17.24 (2.50)  | t = 2.91  |
| ~100 m             | 6             | 10.81 (2.74)  | P = 0.027 |
| Ground             |               |               |           |
| ~25 m              | 2             | 30.25 (12.33) | t = -1.22 |
| ~100 m             | 6             | 37.50 (5.72)  | P = 0.270 |

Table 4. Comparison of faunal similarity and edge effect for each stratum.

| Trap Location                 | Morisita-Horn |             |                      |
|-------------------------------|---------------|-------------|----------------------|
|                               | N             | Mean (SD)   | t Test               |
| Elevated                      |               |             |                      |
| similar distance from edge    | 16            | .710 (.092) | t = .110<br>P = .913 |
| dissimilar distance from edge | 12            | .706 (.090) |                      |
| Ground                        |               |             |                      |
| similar distance from edge    | 16            | .587 (.085) | t = .122<br>P = .904 |
| dissimilar distance from edge | 12            | .583 (.087) |                      |

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## CD REVIEW

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*What wasp is that? An interactive identification guide to the Australasian families of Hymenoptera.* N.B. Stevens, C.J. Stevens, M. Iqbal, J.T. Jennings, J. La Salle & A.D. Austin. Australian Biological Resources Study / Centre for Biological Information Technology (CBIT), 2007. Price: Aus\$64.90. ISBN-13: 978 0 642 56851 9; ISBN-10: 0 642 56851 0

This CD represents a first attempt at an interactive key to the 67 families of Hymenoptera present in Australasia – i.e. Australia, New Zealand and the islands south-east of Wallace's line. In fact, because most of the families treated are cosmopolitan, the key is useful for the majority of Hymenoptera specimens collected anywhere in the world, and this represents a major bonus.

The CD is easy to run, compatible with Windows, Mac OSX, Linux or Solaris, and is based on two Lucid multiple-entry keys with attached html pages. The opening page provides links to the following sections: Introduction, Morphology, Families, Biology & Ecology, Systematics, Collecting, Bibliography and Acknowledgements, as well as the option to immediately enter the main key, or the linked subkey to chalcidoid families.

The introduction is succinct and extremely useful, especially because of the links throughout the text to related information and images. Abundant links are a characteristic of the CD as a whole, both to further information within the CD, but also to other websites, and this is a very helpful feature. The morphology section provides an opportunity to standardise terminology in an area that has historically been prone to multiple terms for the same feature. The section is brief, and could perhaps have been expanded (or can in future editions) to include more information on the female and male genitalia, though admittedly

these are of less importance at the family level. Within this section the chalcidoid family Mymaridae is described as having wings that are “completely veinless”, whereas all Mymaridae have a single vein in the fore wing. Only certain platygastriids can correctly be described as having completely veinless wings. The next section is an A-Z listing of the 67 families treated, with just a couple of paragraphs on each family, together with key references and links. The systematics section provides an overview by superfamily of all the families of Hymenoptera, with links back to the family pages in the previous section, where appropriate. The collecting section is comprehensive and excellent, and even includes information on obtaining collecting permits in Australia, with links to the appropriate websites. There are just a few typos among these pages, listed here to aid preparation of any future edition: Crabronidae, Mymarommatidae, Mutilidae, Plumaridae, Trigonalidae. Megalodontidae should be Megalodontesidae.

Starting the main key, the user has little guidance or advice, and I suspect this could present initial problems for someone unfamiliar with Lucid, or Hymenoptera families, or both. However, a little persistence and experience should enable even a complete novice to successfully identify most families fairly quickly. Certain families are less straightforward to key out, but this can be due to the morphological heterogeneity of their constituent genera (e.g. the chalcid family Aphelinidae). The “magic wand” option within Lucid selects the most discriminatory character, and is therefore recommended. In the case of the main key, following geographical distribution, this is apparently the length of the first discal cell in the fore wing. This choice of character as the most effective one to

start with (after distribution) could be off-putting for a beginner. Following this, the user is then asked whether "hind wing vein *rm* joins *RS* after *RS* has diverged from *SC+R*". The trouble with characters of this degree of complexity is that firstly they discourage the novice, and secondly that by the time they have been mastered, the user is anyway likely to have no difficulty recognising any hymenopteran to family level. It would be an interesting exercise to attempt a key that excludes these kinds of characters, but still works at least 95% of the time. Such a key is far more likely to be widely adopted by non-specialists.

The chalcidoid and mymarommatoid families are in a separate key that can be entered directly, as well as via the general key. An attempt has been made here to present a number of "character suites" that

characterise several families. Again, I would suggest that the beginner faced with this barrage of information required to go one more step could be rather easily put off the whole enterprise.

In summary, the authors have made a first attempt at an extremely demanding task, and have successfully produced a useful and workable product that has relevance globally, and not just to Australasia. The background information and illustrations are well-researched and presented, and the links are invaluable. If the keys were more straightforward to use by non-specialists, this CD could rapidly become a regularly used resource for a far greater audience than is likely to be the case while in its present form.

ANDREW POLASZEK









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**General Policy.** The *Journal of Hymenoptera Research* invites papers of high scientific quality reporting comprehensive research on all aspects of Hymenoptera, including biology, behavior, ecology, systematics, taxonomy, genetics, and morphology. Taxonomic papers describing single species are acceptable if the species has economic importance or provides new data on the biology or evolution of the genus or higher taxon. Manuscript length generally should not exceed 50 typed pages; however, no upper limit on length has been set for papers of exceptional quality and importance, including taxonomic monographs at generic or higher level. All papers will be reviewed by at least two referees. The referees will be chosen by the appropriate subject editor. However, it would be helpful if authors would submit the names of two persons who are competent to review the manuscript. The language of publication is English. Summaries in other languages are acceptable.

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